Postcranial skeleton of a Cretaceous multituberculate mammal *Catopsbaatar*

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We describe an incomplete postcranial skeleton of *Catopsbaatar catopsaloides* from the ?late Campanian red beds of Hermiin Tsav I, in the Gobi Desert, Mongolia. The skeleton is fragmentary and the preservation of bone surface does not permit reconstruction of the musculature. The studied skeleton contains some parts not preserved or incompletely known in other multituberculate genera, such as a long spinous process in a single lumbar vertebra, which together with long transverse processes preserved in *Nemegtbaatar*, might indicate that at least some multituberculates had jumping ability. The calcaneus of *Catopsbaatar* is unusual, differing from most other multituberculates (where known) and other mammals by having a short tuber calcanei, with a large proximal anvil-shaped process strongly bent laterally and ventrally, arranged obliquely with respect to the distal margin of the calcaneus, rather than arranged at 90° to it, as in other mammals. This suggests the presence of strong muscles that attached to the tuber calcanei, perhaps further attesting to jumping abilities in *Catopsbaatar*. We also describe an unfused pelvic girdle and the first extratarsal spur bone (os cornu calcaris) known in multituberculates.

Key words: Mammalia, Multituberculata, Djadochtatheriidae, *Catopsbaatar,* postcranial skeleton, sprawling posture, Cretaceous, Gobi Desert, Hermiin Tsav.

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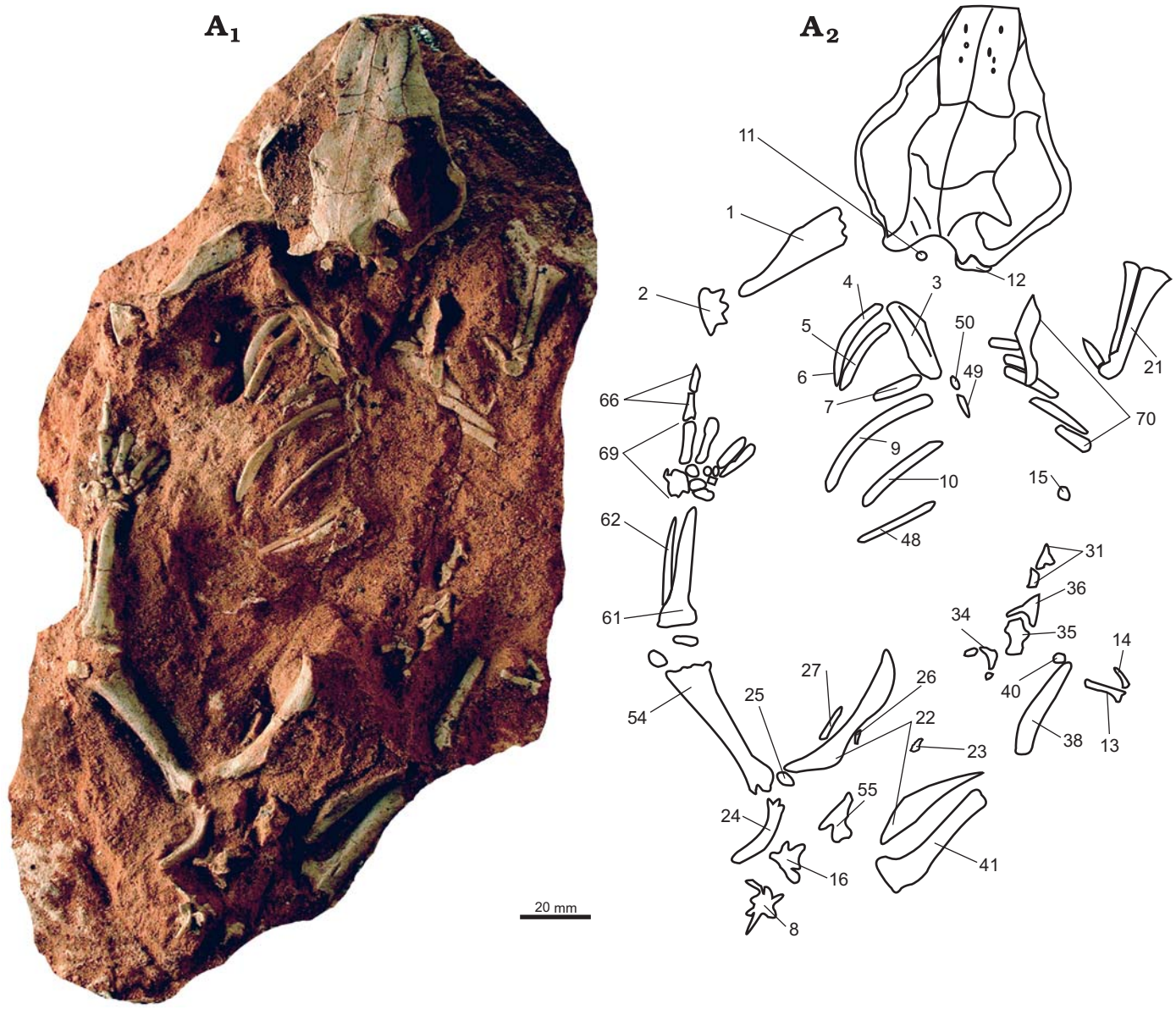
Introduction

Multituberculates are among the most common mammalian fossils in well sampled Cretaceous and Paleocene localities of the Northern Hemisphere, yet parts of the postcranial skeleton are rare. The first comprehensive treatment of the multituberculate postcranial skeleton is that of Krause and Jenkins (1983, see also references therein), who described a nearly complete skeleton of the Paleocene ptilodontoid *Ptilodus kummae,* and revised other postcranial material of North American multituberculates, belonging to the genera *Catopsalis*, *Cimexomys*, *Cimolodon*, *Ectypodus*, *Meniscoessus*, *Mesodma*, *Stygimys*, and *Taeniolabis*. Krause and Jenkins (1983: 200) concluded that "at least some multituberculates were arboreal". Subsequently, Kielan-Jaworowska and Gambaryan (1994) described a number of postcranial elements in three Late Cretaceous djadochtatherioid multituberculate taxa *Kryptobaatar dashzevegi*, *Chulsanbaatar vulgaris*, and *Nemegtbaatar gobiensis*; fragments of the pelvis of *Sloanbaatar mirabilis*; and some tail vertebrae assigned to *Catopsbaatar catopsaloides*, but now regarded as apparently too big to match the size of this species (Kielan-Jaworowska et al. 2002). Kielan-Jaworowska and Gambaryan (1994) provided a partial reconstruction of postcranial musculature of the studied species and offered a new reconstruction of the multituberculate tarsus, different from that of Granger and Simpson (1929), which was generally accepted until that time. They also argued that most of the Asian Cretaceous–Paleocene multituberculates were terrestrial runners, but some of them show adaptations to a fossorial mode of life (Kielan-Jaworowska and Qi 1990).

In the years since publication of the monograph by Kielan-Jaworowska and Gambaryan (1994), some fourteen accounts describing or discussing multituberculate postcranial anatomy have appeared (Presley 1995; Sereno and McKenna 1995, 1996; McKenna 1996; Gambaryan and Kielan-Jaworowska 1997; Rougier et al. 1997; Kielan-Jaworowska 1998; Kielan-Jaworowska et al. 2000, 2002, 2004; Hu et al. 2002a, b; Kielan-Jaworowska and Hurum 2006; Sereno 2006; see also McKenna and Bell 1997).

In the present paper we describe the postcranial skeleton of the Late Cretaceous multituberculate *Catopsbaatar catopsaloides* (Kielan-Jaworowska, 1974) from the locality of Hermiin Tsav I in the Mongolian part of the Gobi Desert, from the so-called red beds of Hermiin Tsav (stratigraphic equivalent of the Baruungoyot Formation, see Kielan-Jaworowska et al. 2002). Our paper is based mostly on a specimen found by Philip Currie during the Nomadic Expedition of 1999 (see Kielan-Jaworowska et al. 2002) and housed in the Paleontological Center of the Mongolian Academy of Sciences in



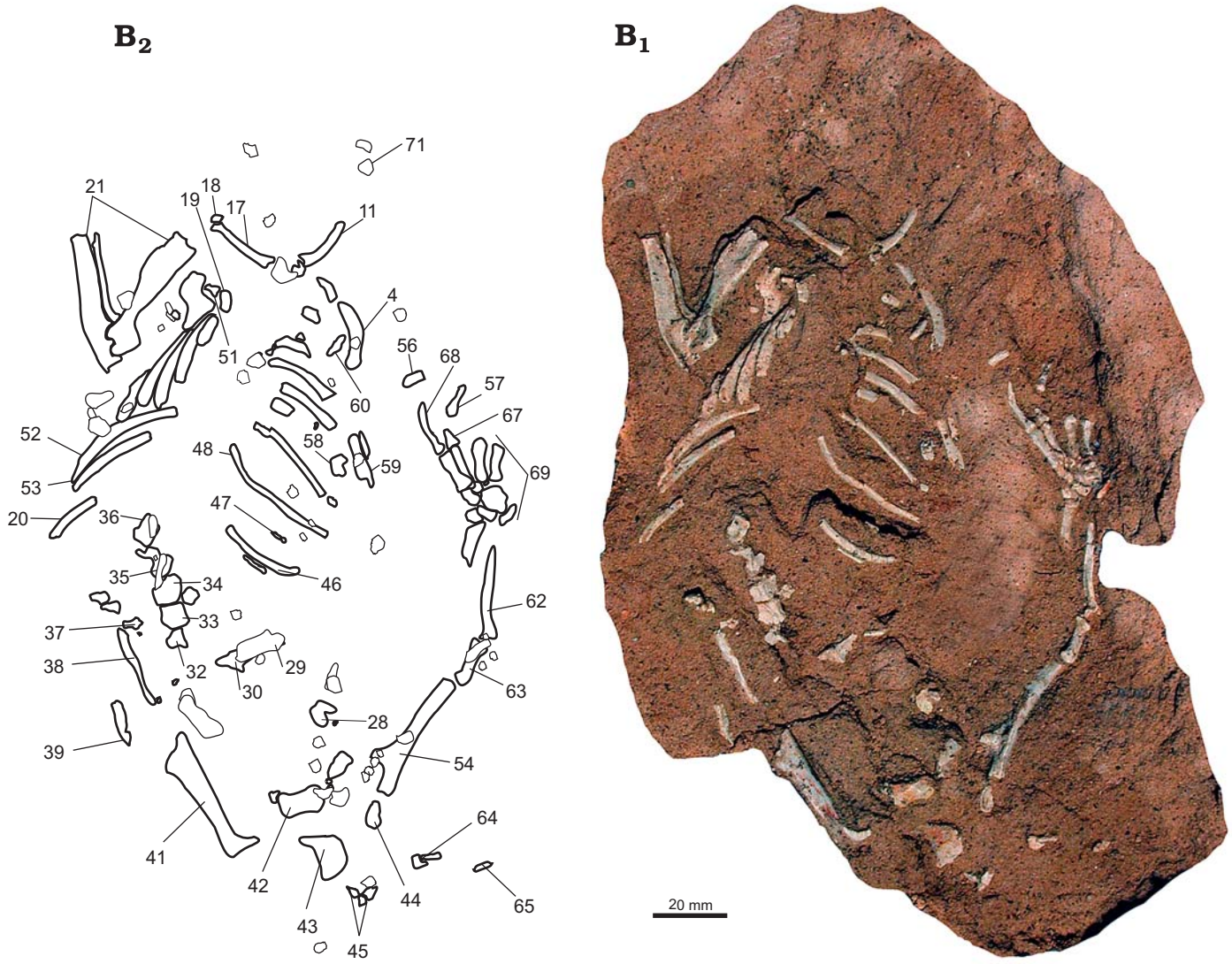
Ulaanbaatar. The skeleton was found in association with skull and mandible, which have been described separately together with other skull specimens of *Catopsbaatar* (Kielan-Jaworowska et al. 2005).

During the preparation of this specimen (see "Material and methods" below) we separated an almost complete right tarsus with partial foot, in which we found os calcaris. We figured this tarsus and foot in the paper by Hurum et al. (2006), dealing with the issue of venomous structures in early mammals. In the present paper we redescribe this tarsus. Elsewhere (Kielan-Jaworowska and Hurum 2006) we discussed the limb posture in multituberculates and other early mammals, figured the os calcaris in *Catopsbaatar* and provided a reconstruction of *Catopsbaatar* as a living animal.

Institutional abbreviations.—BMNH, Natural History Museum, previously British Museum (Natural History), London, Great Britain; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing, China; PM, Paleontological Center of the Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; PSS-MAE, Mongolian-American Museum Expeditions (the collections are for the time being housed at the American Museum of Natural History in New York); UA, University of Alberta, Edmonton, Alberta, Canada; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Material and methods

The postcranial skeleton of *Catopsbaatar catopsaloides* (Kielan-Jaworowska, 1974), which we describe herein (PM 120/107), was embedded in a plaster jacket by Philip Currie,



← Fig. 1. Multituberculate mammal *Catopsbaatar catopsaloides* (Kielan-Jaworowska, 1974), PM 120/107, Upper Cretaceous, red beds of Hermiin Tsav, Hermiin Tsav I locality, Gobi Desert, Mongolia. General views of the skeleton, as preserved, before separation of particular bones. **A**. Dorsal view. **B**. Ventral view of the same, after separation of the skull and some bones. Explanation of the numbers: 1, left humerus; 2, head of ulna; 3, left scapulacoracoid; 4, rib from left side; 5, rib from left side; 6, rib from left side; 7, rib from left side; 8, incomplete lumbar vertebra; 9, rib from left side; 10, rib from left side; 11, left clavicle; 12, fragment; 13, right metatarsal; 14, right metatarsal; 15, fragment; 16, incomplete lumbar vertebra; 17, right clavicle; 18, fragment; 19, fragment; 20, right rib; 21, right humerus, radius and ulna ; 22, left and right ilia (now missing); 23, fragment; 24, left ischium; 25, fragment; 26, fragment; 27, prepubis; 28, fragment; 29, fragment ; 30, Os cornu calcaris; 31, incomplete vertebra; 32, incomplete vertebra; 33, incomplete vertebra; 34, incomplete vertebra; 35, incomplete vertebra; 36, incomplete vertebra; 37, fragment; 38, right tibia; 39, ?fibula; 40, fragment; 41, right femur; 42, right pubis; 43, right ischium; 44, fragment; 45, fragments; 46, left rib; 47, fragments; 48, left rib; 49, fragment; 50, fragment; 51, fragment ; 52, right rib; 53, right rib; 54, left femur; 55, incomplete lumbar vertebra; 56, phalange from left foot; 57, phalange from left foot from III; 58, fragment of rib; 59, fragments of ribs; 60, fragment of ?scapulacoracoid; 61, left tibia; 62, left fibula; 63, left Vth metatarsal with first phalange ; 64, fragments; 65, fragment; 66, phalanges from left foot from IV; 67, phalanges from left foot from II; 68, phalanges from left foot from I; 69, left tarsus, proximal part; 70, right ribs and scapulacoracoid associated: 71, right astragalus.

who found it. The matrix and the bones exposed after removal of the dorsal layer of the plaster jacket were figured by Kielan-Jaworowska et al. (2002: fig. 1), and are refigured herein (Fig. 1A). We separated all the bones and bone fragments of the postcranial skeleton (103 altogether), of which the majority represents unidentifiable fragments, or incomplete and poorly preserved parts (e.g. middle parts of ribs, or fragments of vertebrae). These damaged fragments do not merit description or illustrations and we describe and figure only the more completely preserved parts.

We follow the anatomical terminology of Krause and Jenkins (1983) and Kielan-Jaworowska and Gambaryan (1994). Please note that we refer to the figures in this paper using capital letters (for example Fig. 1A, Fig. 2), while the figures from other papers with lower case letters (for example Krause and Jenkins 1983: figs. 1, 2).

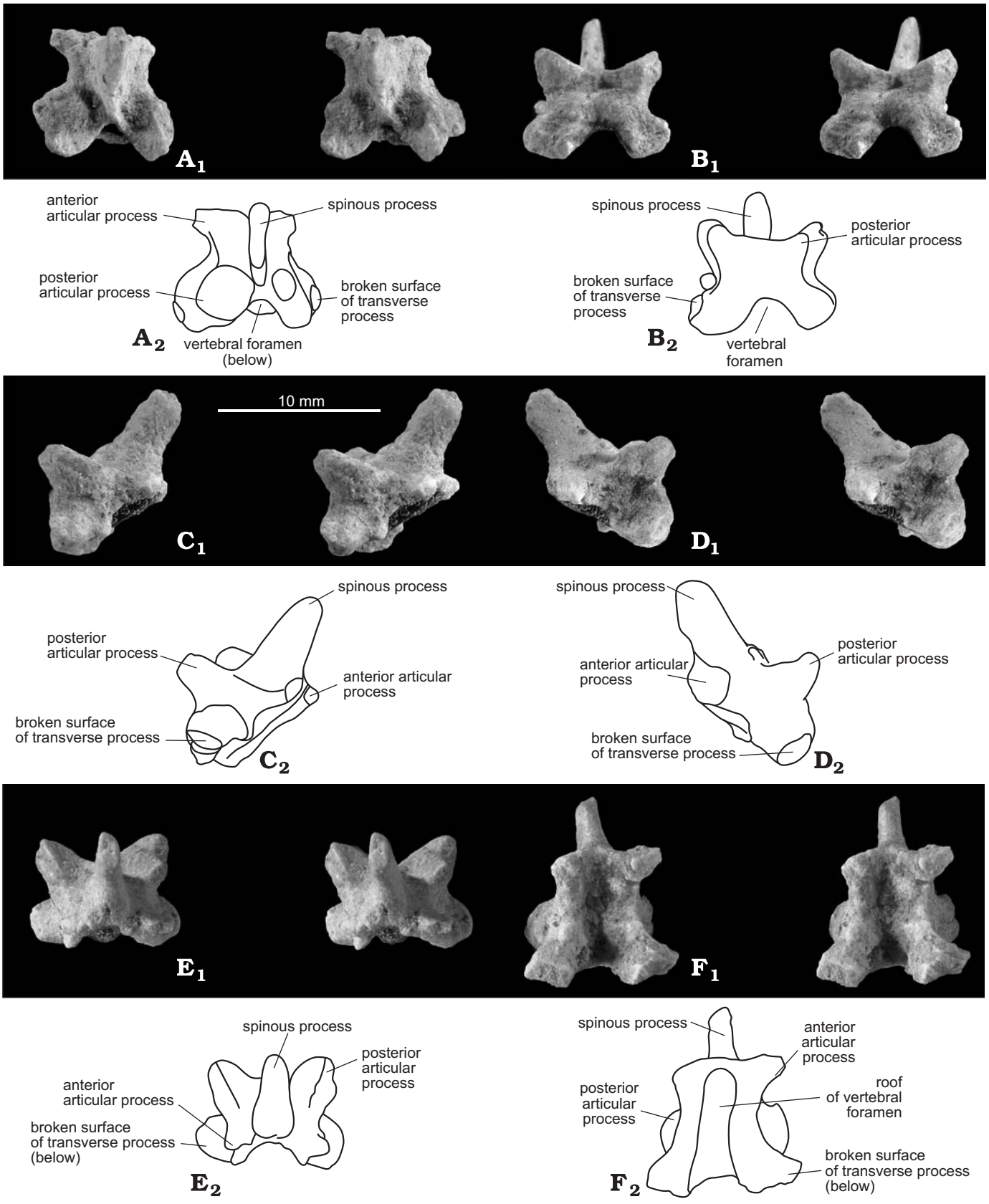


Fig. 2. Multituberculate mammal *Catopsbaatar catopsaloides* (Kielan-Jaworowska, 1974), PM 120/107, Upper Cretaceous, red beds of Hermiin Tsav, Hermiin Tsav I locality, Gobi Desert, Mongolia. Incomplete lumbar vertebra (possibly L5 or L6), with spinous process partly preserved, missing transverse processes and the body (no. 8 in Fig. 1A), in dorsal (**A**), posterior (**B**), right lateral (**C**), left lateral (**D**), anterior (**E**), and ventral (**F**) views. Stereo-photographs (A_1, B_1, C_1, D_1, E_1, and F_1) and explanatory drawings (A_2, B_2, C_2, D_2, E_2, and F_2). All the items are in the same scale (marked at C_1).

Table 1. Measurements of the bones of *Catopsbaatar catopsaloides* PM 120/107. We have measured only the bones that are completely preserved.

	Number in Fig. 1	Max. length [mm]	Max. width [mm]
Skull		63	55
Dentary		41	9
Clavicle (left)	11	24.8	2
Pubis	42	11.4	7.3
Ischia	43	17.8	13.7
Tibia (left)	61	35.8	3 (shaft mediolaterally) 7 (shaft anterioposteriorly)
Fibula (left)	62	30	3.2 (anterioposteriorly) 2.1 (mediolaterally
Calcaneus	69	11.4	7.2
Os cornu calcaris	69	13	5
Astragalus	69	7	5
Metatarsal 1	69	12.1	2
Metatarsal 2	69	12	2
Metatarsal 3	69	11.5	2
Metatarsal 4	69	11.2	1.9
Metatarsal 5	63	13	2

Descriptions

Axial skeleton

Catopsbaatar catopsaloides (Kielan-Jaworowska, 1974, if not stated otherwise the descriptions that follow are of the specimen PM 120/107).

The vertebral column has been virtually weathered away. The cervical, thoracic, and lumbar vertebrae (except for the incomplete lumbar vertebra illustrated in Fig. 2, and some unidentified fragments) are missing. Kielan-Jaworowska et al. (2002: fig. 1) designated as "vertebrae" the bone fragments preserved in the second half of the exposed specimen (nos. 49 and 50 in Fig. 1A). We now recognize these fragments (see our Fig. 1A) as parts of the sternum, which are, however, too fragmentary to merit description. There are three fragments of vertebrae of which only one merits description (no. 8 in Fig. 1A).

Only the upper part of the vertebra has been preserved. By comparison with the lumbar vertebrae of *Nemegtbaatar* (Kielan-Jaworowska and Gambaryan 1994: fig. 11), we suggest that our specimen represents the fifth or sixth lumbar vertebra. The spinous process is stout in lateral view and long, arranged obliquely antero-dorsally. Although it is not completely preserved, the topmost part being missing, its size indicates that of the two reconstructions of the length of the spinous process in *Nemegtbaatar gobiensis*, offered by Kielan-Jaworowska and Gambaryan (1994: fig. $36B_2$, dashed and dotted lines in L5 and L6), the one expressed by dashed lines corresponds more closely to the length characteristic of *Catopsbaatar catopsaloides*. As a comparable length has also been preserved in Cd1 of *Kryptobaatar dashzevegi* (Kielan-Jaworowska and Gambaryan 1994: fig. 2, the spinous processes of L6 and L7 being incomplete in this specimen), we concur with the conclusion of Kielan-Jaworowska and Gambaryan (1994) that at least djadochtatherioid multituberculates had a long spinous process on lumbar vertebrae (contra Sereno 2006). We conclude that *Catopsbaatar* might have had jumping abilities (see illustrations in Slijper 1946).

Shoulder girdle and forelimb

Of the shoulder girdle only the clavicles and scapulocoracoids are preserved, and of the forelimb two incomplete humeri, one of them associated with radius and ulna.

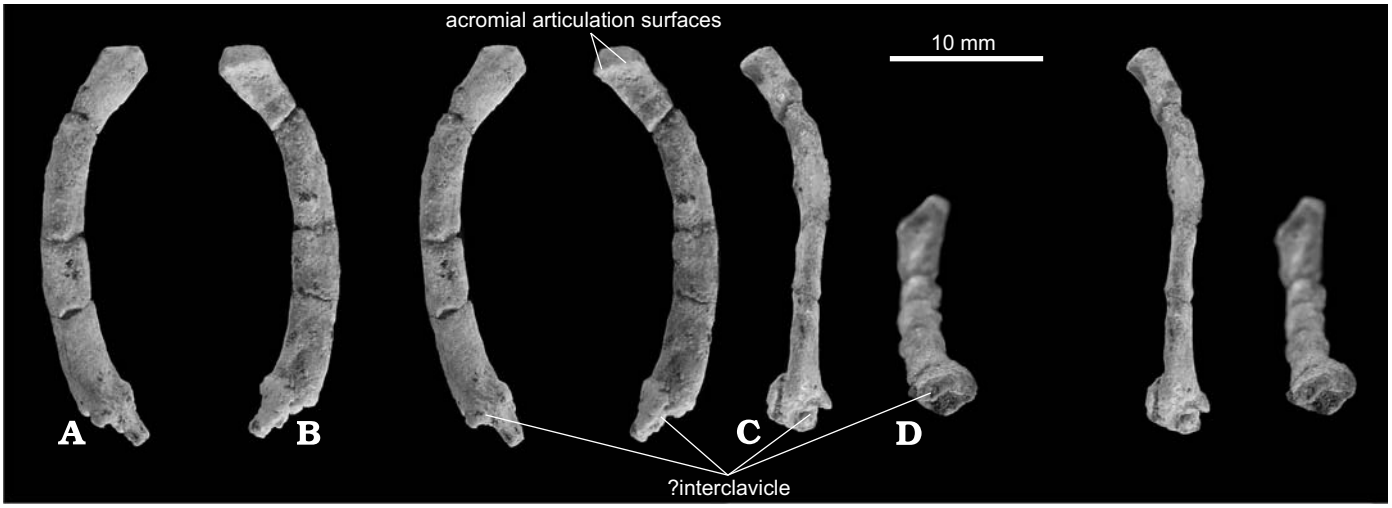


Fig. 3. Multituberculate mammal *Catopsbaatar catopsaloides* (Kielan-Jaworowska, 1974), PM 120/107, Upper Cretaceous, red beds of Hermiin Tsav, Hermiin Tsav I locality, Gobi Desert, Mongolia. Left clavicle, associated with a tiny fragment of ?interclavicle (no. 11 in Fig. 1B). Stereo-photographs in anterior (**A**), posterior (**B**), and medial (**C**) views. **D**. Stereo-photo of the articular medial surface, showing damaged fragment of ?interclavicle.

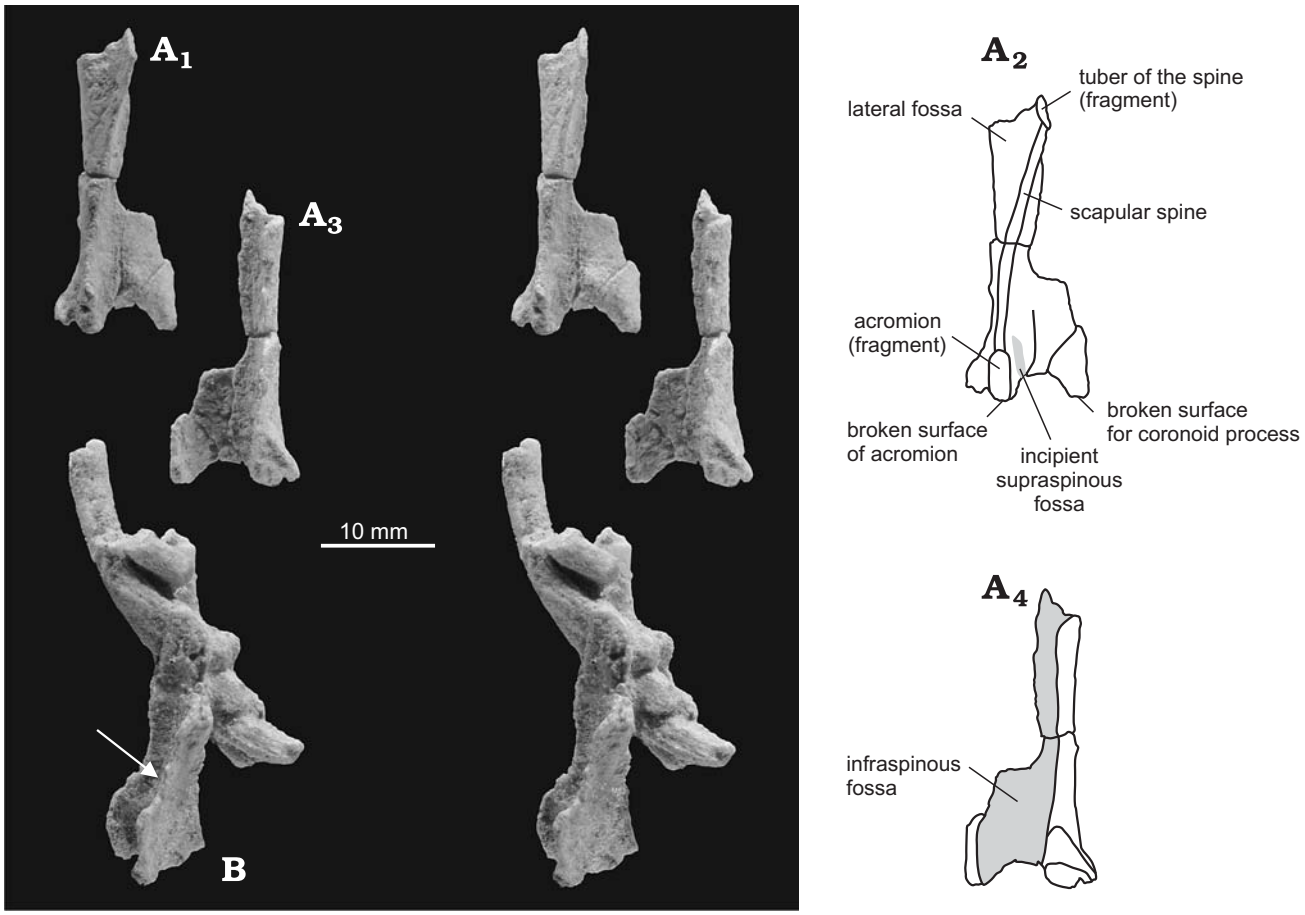


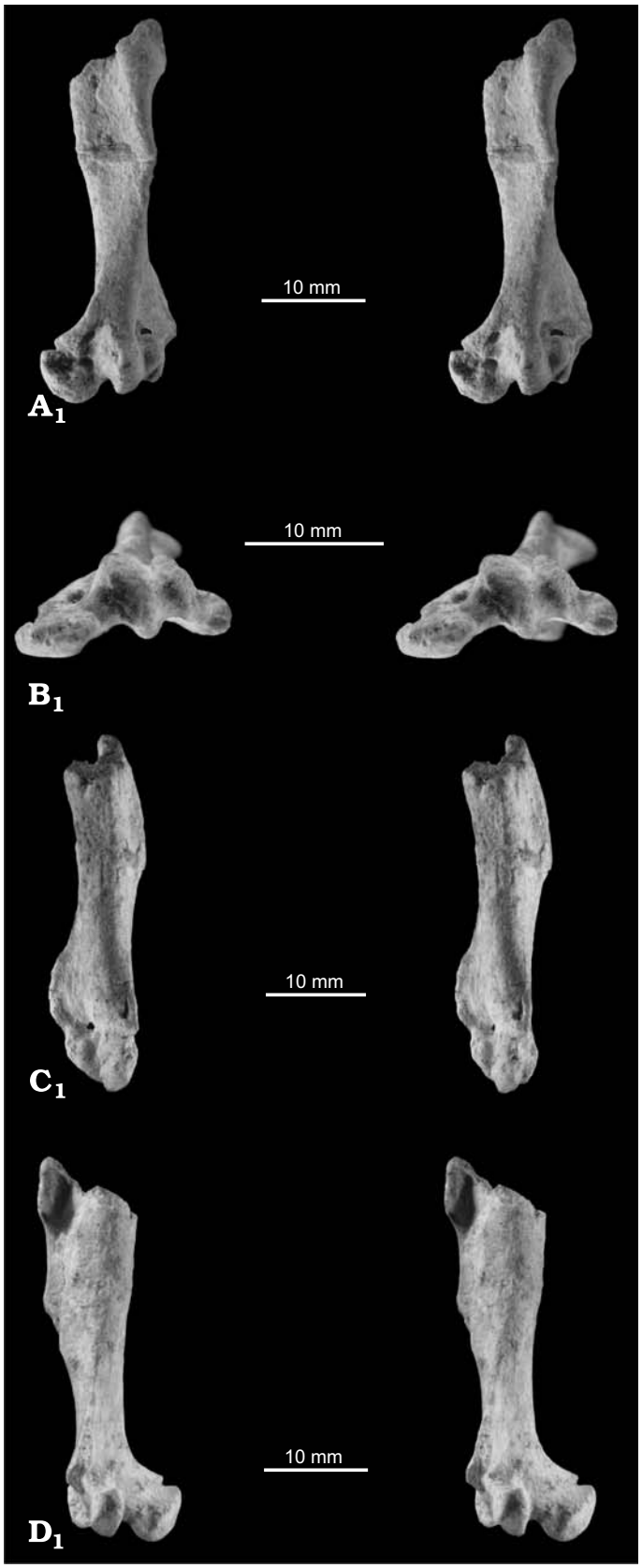
Fig. 4. Multituberculate mammal *Catopsbaatar catopsaloides* (Kielan-Jaworowska, 1974), PM 120/107, Upper Cretaceous, red beds of Hermiin Tsav, Hermiin Tsav I locality, Gobi Desert, Mongolia. **A**. Scapulocoracoid fragments (no. 3 in Fig. 1B) of the left incomplete scapulocoracoid in lateral view (A_1), and explanatory drawing of the same (A_2), in medial view (A_3) and explanatory drawing of the same (A_4). **B**. Displaced fragment of the right scapulocoracoid (no. 70 in Fig. 1B), associated with broken and displaced ribs; the scapulocoracoid in anteromedial view; the arrow points to the infraspinous fossa. A_1, A_3, and B, stereo-photographs.

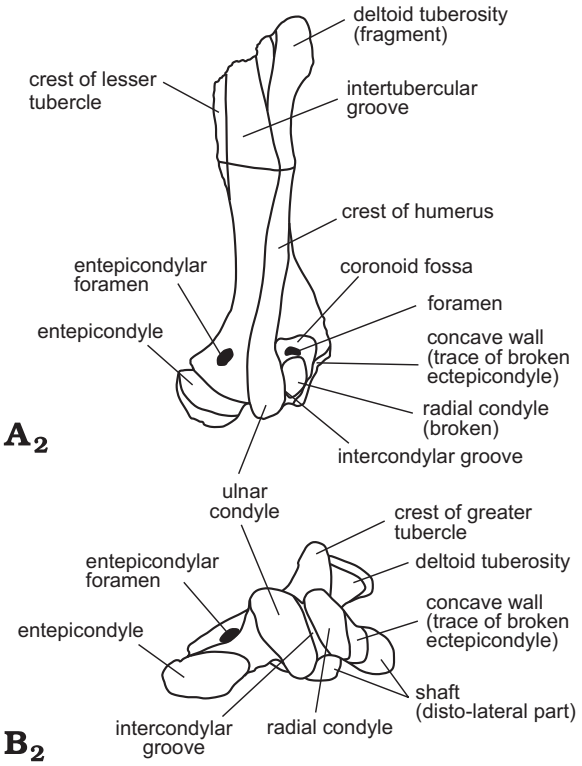
Clavicle.—The clavicles are nearly complete, though strongly damaged in PM 102/107 (nos. 11 and 17 in Fig. 1B; see also Fig. 3).

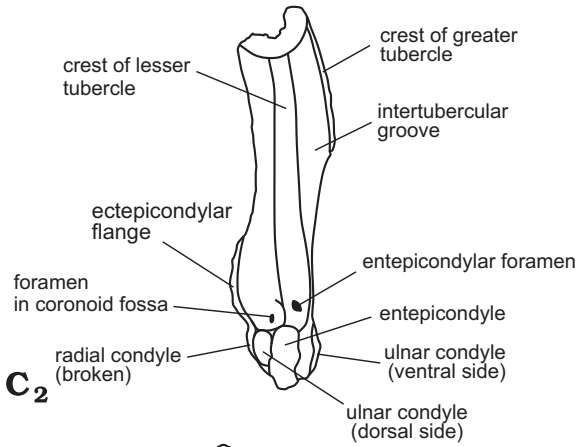
The only multituberculate clavicles so far described and figured are preserved on both sides of *Kryptobaatar dashzevegi* Kielan-Jaworowska, 1970, PSS MAE-103, from the ?early Campanian Djadokhta Formation of Bayan Zag, Gobi Desert, Mongolia (Sereno 2006). The specimen was figured and discussed earlier by Sereno and McKenna (1995) and referred to as cf. *Bulganbaatar nemegtbaataroides* Kielan-Jaworowska, 1974.

Sereno (2006: 326) described the clavicles of *Kryptobaatar* as follows: "The clavicles are slender rod-shaped elements that curve from the acromion to the midline, where they presumably articulate in a pair of shallow fossae on the anterior face of the interclavicle (fig. 10.4). The left and right clavicle have been dislodged ventrally and dorsomedially, respectively (fig. 10.4). The fossae are broadly open, and the joint, for this reason, appears to have allowed pivoting movement of the clavicle in several directions. The lateral half of the clavicle is dorsoventrally flattened and curves posteriorly toward the acromion and over the bulbous head of the humerus. There does not appear to be any contact between the clavicle and humeral head."

Each of the two clavicles preserved in PM 102/107 consists of several fragments, which have been glued together. For this reason, the left clavicle (Fig. 3A) appears more curved than the right one, but this is due to the inaccuracy of the gluing of the tiny parts together. Because of the poor state of preservation of the right clavicle, we figure here only the left one. As a whole the clavicle of *Catopsbaatar* might have been slightly less curved than that of *Kryptobaatar* (Sereno 2006: figs. 10.3, 10.7A–C). The length of the left clavicle in *Catopsbaatar* (Fig. 3) along the chord (geom) is about 24.8 mm. The clavicle resembles a bent rod, slightly widened at both ends. The lateral (acromial) end is asymmetrical, slightly pointed, and consists of two small flat surfaces separated by a faint ridge and arranged at an angle of about 45°. The lateral surface is larger than the one facing ventrally. At the medial ends of both clavicles damaged fragments of the ?interclavicles have been preserved, the larger fragment associated with the right clavicle, a very tiny one with the left.







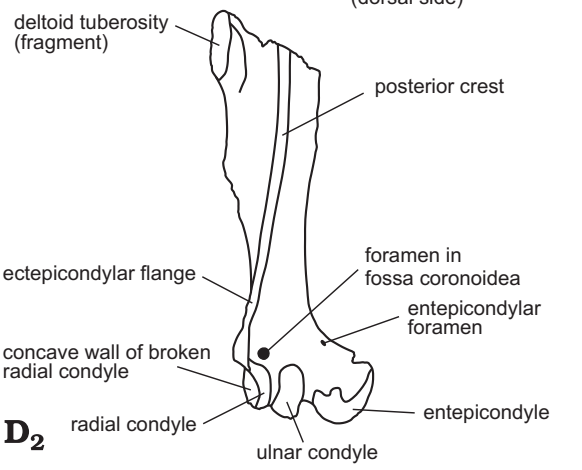


Fig. 5. Multituberculate mammal *Catopsbaatar catopsaloides* (Kielan-Jaworowska, 1974), PM 120/107, Upper Cretaceous, red beds of Hermiin Tsav, Hermiin Tsav I locality, Gobi Desert, Mongolia. Incomplete left humerus (no. 1 in Fig. 1A). Middle and distal parts of the humerus in anterior (ventral) (**A**), distal (**B**), medial (**C**), and posterior (dorsal) (**D**) views. Stereo-photographs (A_1, B_1, C_1, D_1) and explanatory drawings (A_2, B_2, C_2, D_2). Note that B is in a different scale than A, C, and D.

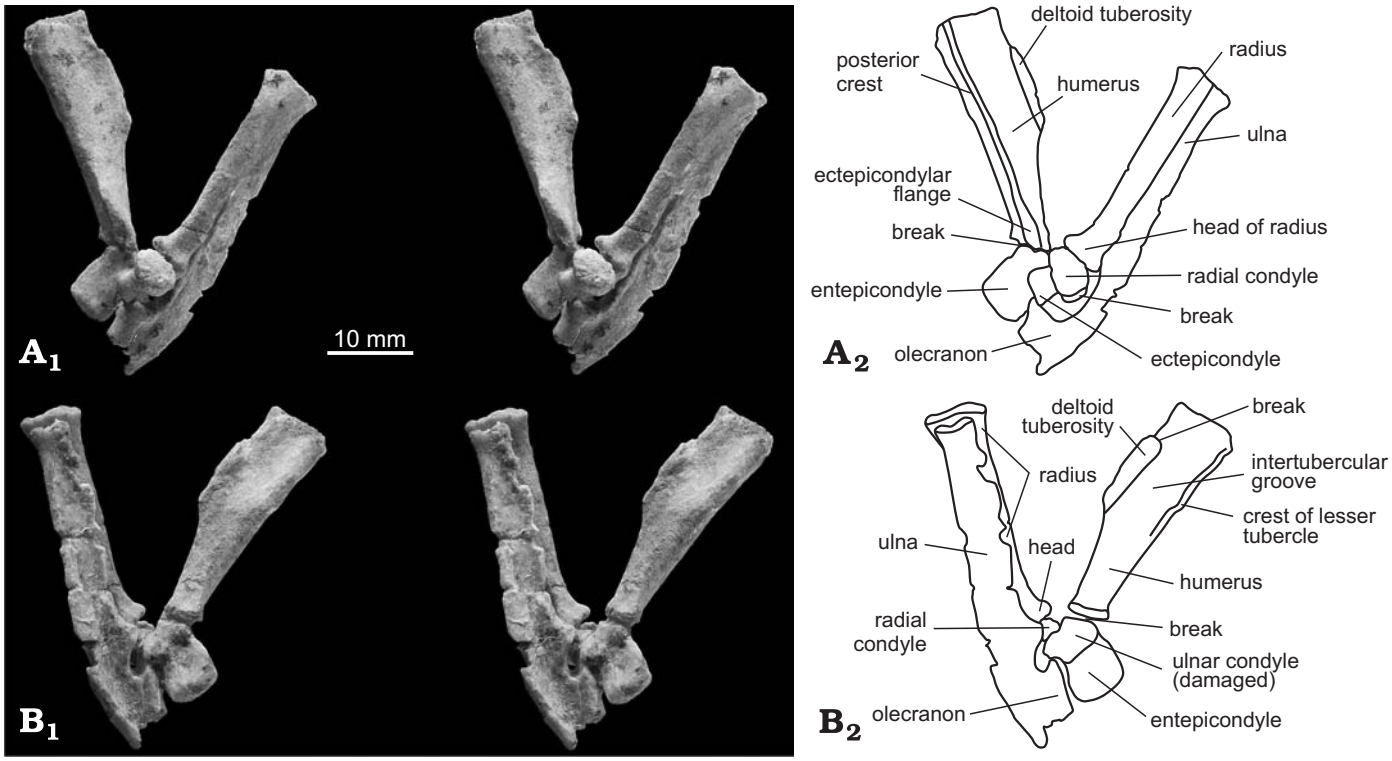


Fig. 6. Multituberculate mammal *Catopsbaatar catopsaloides* (Kielan-Jaworowska, 1974), PM 120/107, Upper Cretaceous, red beds of Hermiin Tsav, Hermiin Tsav I locality, Gobi Desert, Mongolia (no. 21 in Fig. 1A and B). Incomplete right humerus in association with radius and ulna. **A**. Dorsal view. **B**. Ventral view. Stereo-photographs (A_1, B_1) and explanatory drawings of the same (A_2, B_2).

Scapulocoracoid.—Parts of both scapulocoracoids are preserved in PM 120/107 (nos. 3 and 70 in Fig. 1A, and no. 60 in Fig. 1B), of which the isolated left one is more complete (Fig. 4A), than the right, which is associated with several ribs (Fig. 4B). In both scapulocoracoids the coracoid processes are broken, and in the left one the fragment of the dorsal part of the acromion has been preserved (missing in right scapulocoracoid). The preserved part of the left scapulocoracoid is about 27 mm long. By comparison with complete scapulocoracoids preserved in *Kryptobaatar dashzevegi* (PSS-MAE 103), one can estimate the length of the entire scapulocoracoid as about 60 mm.

In lateral[1] view the left scapulocoracoid is relatively wide proximally, due to the enlarged acromial and coracoid parts, and very narrow distally (dorsally). Extending dorsally from the preserved fragment of acromion is the scapular spine with the fragment of the tuber of the spine (Schaller 1992: 48–49), only the ventral part of which has been preserved in the most dorsal part of the preserved fragment of the spine. In lateral view the spine extends obliquely across the blade, reaching the medial margin of the blade dorsally. In lateral view of the left scapulocoracoid (Fig. 4A_1, A_2) anterior to the spine, there extends a narrow, roughly triangular fossa, referred to by Sereno (2006) for *Kryptobaatar* as the lateral fossa. The infraspinous fossa, which is very deep and trough-like, is not seen in lateral view (a condition seen in other multituberculates), being exposed in anterior and medial views (Fig. 4A_3, A_4).

In the proximal (ventral) part of the scapulocoracoid, between the bases of the broken acromion and coracoid processes, the ventral margin of the blade is concave, and above it there is a small depression, referred to as an incipient supraspinous fossa.

Humerus.—The distal ends are incomplete and the proximal ends are missing from both humeri of PM 120/107 (Figs. 5, 6). The left humerus has been preserved separately, posterolaterally to the left side of the skull (no. 1 in Fig. 1A), while the right one has been preserved to the rear of the right side of the skull, in articulation with the radius and ulna (no. 21 in Fig. 1B).

The preserved part of the left humerus (Fig. 5) is about 37.5 mm long. The shaft is triangular in cross-section, relatively narrow in anterior view, most of its width being occupied by the wide intertubercular groove. The groove is delimited laterally by the crest of the greater tubercle, the middle part of which forms the deltoid tuberosity (Schaller 1992 = the delotopectoral crest of other authors), on the lateral surface of which musculus deltoideus inserts. The crest

[1] McKenna (1961) discussed the ambiguity concerning the orientation of the multituberculate shoulder girdle. He stated (p. 3): "The orientation that seems the most practical for the multituberculate scapulocoracoids under discussion is that in which scapular spine projects laterad. The description can be written consistently, and I hope clearly in that orientation". We follow McKenna in this respect.

is narrow and high in the middle of its course, where it slightly overhangs the lateral surface, distally it continues as the crest of the humerus and becomes wider, less sharp, and lower; it reaches the ulnar condyle and merges into it. The crest of the lesser tubercle is less prominent than that of the greater tubercle. In anterior view the proximal part of the intertubercular groove is parallel-sided and roughly triangular-shaped distally; the distal extremity is very wide and prominent.

The ectepicondyle is missing in this specimen, and the radial condyle is incompletely preserved, divided by a break into two parts, giving impression that the radial condyle was relatively small, rather than large, bulbous-shaped, as preserved in the right humerus (Fig. 6A). The lateral side of the distal extremity of the left humerus is formed by the concave lateral wall of the broken radial condyle, originally continuous with the missing ectepicondyle. The ectepicondyle preserved in the right humerus (see below) is small, roughly rectangular, and much smaller than the entepicondyle. The radial condyle as preserved in the left humerus is incomplete and therefore appears smaller than the ulnar condyle, and oval-shaped in anterior view (Fig. 5B, C). It is ball-shaped in the right humerus (see below) but relatively less prominent than in e.g., *Lambdopsalis* (Kielan-Jaworowska and Qi 1990; Kielan-Jaworowska and Gambaryan 1994; Gambaryan and Kielan-Jaworowska 1997). The ulnar condyle, as preserved in the left humerus, is oval-shaped and wider than the incomplete radial condyle, and protrudes more distally than the radial condyle. The entepicondyle is very large, fan-shaped, and protrudes strongly both medially and distally. Along the proximo-medial border of the entepicondyle there is an obliquely arranged entepicondylar foramen, as characteristic of multituberculate humeri. The fossa coronoidea (olecranon fossa), as usually, is present above the two condyles, perforated by a foramen. The intercondylar groove is extremely narrow.

In posterior view of the left humerus (Fig. 5D) the ulnar condyle is more prominent than the radial condyle, oval-shaped, and delimited from the radial condyle by a deep groove. The posterior crest is visible at the proximal part of the humerus; distally it passes into a prominent ectepicondylar flange. The teres tubersosity, characteristic of other multituberculate humeri, has not been preserved.

The right humerus (Fig. 6) has been broken transversely proximal to the entepicondylar foramen. The distal part has been additionally broken and displaced along the intercondylar groove, and the radial condyle and associated ectepicondyle have been rotated about 180° with respect to the entepicondyle and the ulnar condyle (Fig. 6A). The ulnar condyle appears incomplete, apparently reduced in size due to the preservation. It is visible in ventral view, placed close to the articular surface for the ulnar condyle very close to the semilunar notch of the ulna, but not articulating with it. The ball-shaped radial condyle is visible in the dorsal view in articulation with the head of the radius. It is situated close to the articular surface for the radial condyle in the semilunar notch of the ulna, but does not articulate with it. A small, peg-like ectepicondyle has been preserved in prolongation of the radial condyle, visible in dorsal view (Fig. 6A), where, due to displacement, it covers partly the entepicondyle and contacts the distal part of the olecranon process of the ulna.

The details of the shaft structure are almost a mirror image of those of the left humerus. The only difference is that in the left humerus the deltoid tuberosity is more completely preserved, higher and more strongly overhangs the intertubercular groove.

Radius.—The right radius preserved in PM 120/170 (Fig. 6) in association with the ulna and the distal part of the humerus, appears almost complete, with one subtransversal break close to the radial head. The radius (measured in dorsal view) is 26 mm long. The radial head is prominent, asymmetrical as seen in dorsal view, more strongly protruding over the body of the radius medially than laterally, and 5.3 mm wide. The articulating surface of the radial head (fovea of the head) is not visible, being obscured by the radial condyle of the humerus, which articulates with it. The articular circumference (for articulation with the radial notch of the ulna) is not discernible. The neck of the radius is better marked in dorsal than in ventral view. The body (shaft) of the radius is smooth in dorsal and ventral views, with smooth medial and lateral borders. It is compressed dorsoventrally, slightly bent ventrally in distal part, oval in cross-section, and much less flat than the body of the ulna. Distally the body of the radius enlarges in mediolateral width, forming the trochlea of the radius, which reaches the greatest diameter at the surface for articulation with carpal bones. The trochlea, in both dorsal and ventral views appears asymmetrical, more protruding medially than laterally. Its width is 7.0 mm, exceeding that of the head. In distal view (not figured) the surface for articulation with the carpal bones is divided into two parts. The lateral part forms a flat, oval surface that is 5 mm lateromedially and 3 mm dorsoventrally. The remaining medial 2 mm of the surface is roughly triangular, measuring 1.5 mm at the contact with the oval surface and tapering towards the medial border. It is directed obliquely with respect to the flat oval surface, which is well visible in dorsal view of the radius (Fig. 6A). As both surfaces are poorly preserved, no further details can be discerned, the styloid process not being recognized.

Ulna.—The right ulna (Fig. 6) is almost complete, but damaged, having the body strongly flattened dorsoventrally, with three transverse cracks; the medial margin (as seen in ventral view Fig. 6B) shows several bone defects, and the tip of the olecranon process is broken off. The preserved part of the ulna is about 40 mm long. The preserved part of the olecranon is oriented along the long axis of the body (shaft) of the ulna, its width is about 7.3 mm. The lateral margin of the olecranon process is slightly bent medially; in ventral view the process is distinctly concave, with strongly thickened lateral border; in dorsal view the olecranon process is slightly

convex. The details of the structure of the semilunar notch are obscured by the displaced and broken parts of the distal extremity of the humerus. In dorsal view the radius and the radial condyle (associated with ectepicondyle) fill the semilunar notch, while in ventral view the damaged ulnar condyle touches the notch. At the distal margin of the semilunar notch the small coronoid process is seen in ventral view. The body of the ulna distal to the coronoid process is 6 mm wide; it has straight lateral and medial margins and decreases in width distally. The distal extremity of the ulna measures 2 mm mediolaterally and 4 mm dorsoventrally. As preserved together with the radius, the distal end of the ulna is narrower and shorter than that of the radius (Fig. 6B), as characteristic of most mammals (Lessertisseur and Saban 1967).

Pelvic girdle and hind limb

As may be seen in Kielan-Jaworowska et al. (2002: fig. 1) and Fig. 1A in this paper, originally both ilia and ischia were preserved in PM 120/107. Unfortunately, when the specimen was prepared in the Natural History Museum, University of Oslo, in 2000, the ilia developed from the rock have been stolen and destroyed by a school boy during the course of a tour. Notwithstanding efforts of the Museum authorities, it proved impossible to find and recover the stolen part.

Ischium.—The left and right ischia are present in the specimen. The right ischium (no. 43 in Fig. 1B) is better preserved than the left one, but the left one shows the more complete length of the ischium. The right ischium (Fig. 7A) has no attachment zone for the left ischium. The postobturator notch and the part of the obturator foramen limited by the ischium are well defined. The contact to the ilium and pubis is not fused and the anterior end of the ischium forms a rugose suture (Fig. 7A). There is no trace of a smooth acetabulum in the anterior end. The left ischium (no. 24 in Fig. 1A) lacks more of the large posterior flange, but the contact to the ilium is identical.

Pubis.—The right pubis is preserved (no. 42 in Fig. 1B and Fig. 7B) it is a roughly rectangular bone with a rough suture for the ilium at its dorsal end and a deep groove for the ischium in its anteroventral part. There is no trace of a notch for an prepubis though one is known to be present in other multituberculates (Kielan-Jaworowska and Gambaryan 1994 and references therein) and we tentatively identify a fragment of one in this specimen (no. 27 in Fig. 1A).

Ilium.—The right and left ilia (no. 22 in Fig 1A) are now lacking and can only be reconstructed on the basis of the photographs taken during preparation. The left ilium was complete and about 45 mm long. In dorsal view it was wider anteriorly and posteriorly than at the middle.

Hind limb

Of the hind limbs the right and left partial femora, right and left tibiae, left fibula, left tarsus and part of the foot have been preserved. The bones of the left hind limb are preserved in anatomical arrangement (see Fig. 1), but in spite of this, the distal and proximal parts of the long bones have been broken.

Femur.—Gidley (1909) was the first to publish on multituberculate postcranial skeleton (from the Paleocene of North America); subsequent accounts are given by Granger and Simpson (1929) and Krause and Jenkins (1983), who de-

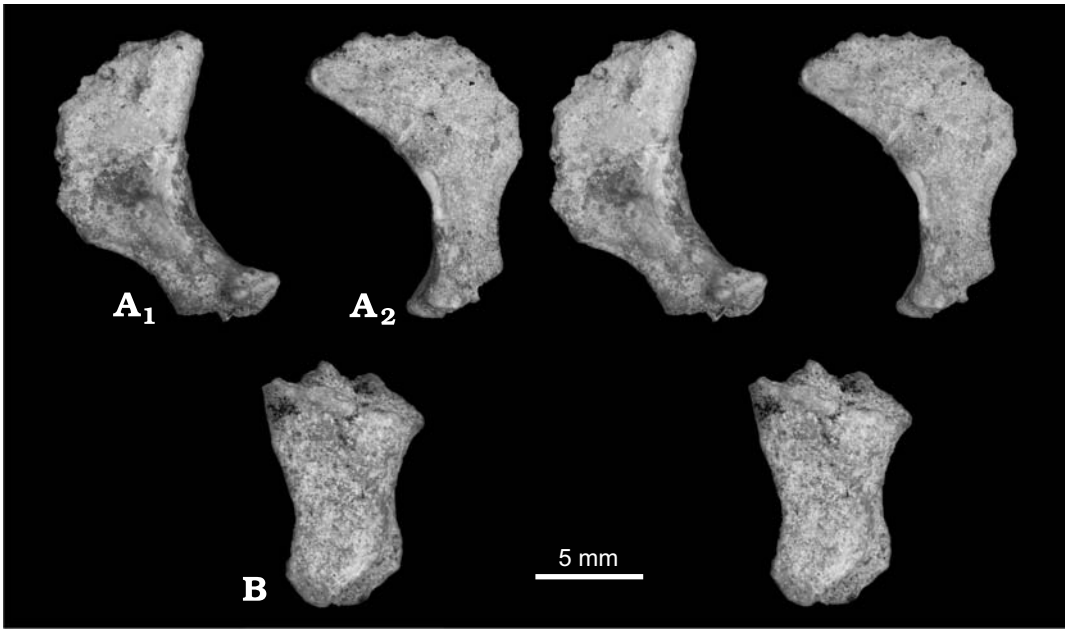


Fig. 7. Ischia and pubis of *Catopsbaatar catopsaloides* (Kielan-Jaworowska, 1974), PM 20/107, Upper Cretaceous, red beds of Hermiin Tsav, Hermiin Tsav I locality, Gobi Desert, Mongolia. **A**. Right ischium (no. 43 in Fig. 1B) in lateral (A_1) and medial (A_2) views. **B**. ?left pubis (no. 42 in Fig. 1B) in lateral view. All stereo-photographs.

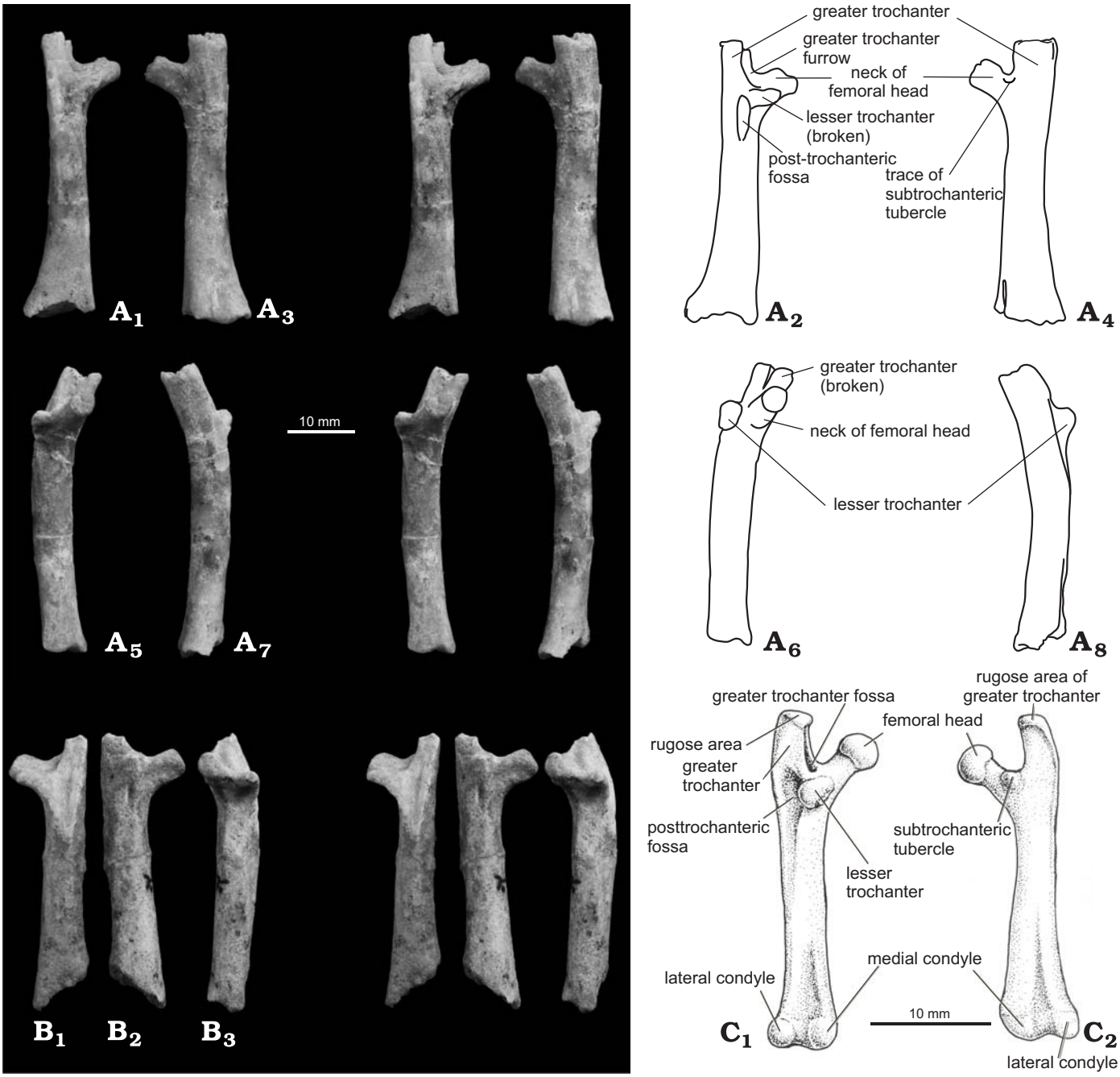


Fig. 8. Multituberculate mammal *Catopsbaatar catopsaloides* (Kielan-Jaworowska, 1974), PM 120/107, Upper Cretaceous, red beds of Hermiin Tsav, Hermiin Tsav I locality, Gobi Desert, Mongolia. Incomplete femora. **A**. Left femur (no. 54 in Fig. 1B) in ventral (A_1, A_2), dorsal (A_3, A_4), medial (A_5, A_6), and lateral (A_7, A_8) views. **B**. Right femur (no. 41 in Fig. 1A and 1B), in ventral (B_1), dorsal (B_2), and medial (B_3) views. **C**. Reconstruction of multituberculate femur based on *Kryptobaatar*, *Nemegtbaatar*, and *Eucosmodon*, shown for comparison, in ventral (C_1) and dorsal (C_2) views. Stereo-photographs (A_1, A_3, A_5, A_7, B_1–B_3) and explanatory drawings (A_2, A_4, A_6, A_8).

scribed all the North American multituberculate Late Cretaceous and Paleocene postcranials known at that time. Kielan-Jaworowska and Gambaryan (1994) described Late Cretaceous femora from the Gobi Desert, the best preserved of which belong to *Kryptobaatar dashzevegi* and *Nemegtbaatar gobiensis*.

The two femora preserved in *Catopsbaatar catopsaloides* (PM 120/107) are incomplete. The left femur (Fig. 8A) includes the femoral shaft, the neck of the head, and basal part of the greater trochanter. The lesser trochanter (which is either broken or eroded) is less prominent than in well preserved femora of other taxa; the same concerns the subtrochanteric tubercle, which is hardly discernible. The distal part is also incomplete, the shaft has been broken at the place where its width increases, and the condyles have been broken off. However, the lateral condyle has been preserved fused to

the proximal part of the left tibia (Fig. 9A$_1$–A$_2$). The right femur (Fig. 8B) is slightly less complete than the left one, and it does not preserve parts missing in the left.

The femur of *Catopsbaatar* is generally similar in proportions to ?*Eucosmodon* sp. (AMNH 16325, see Krause and Jenkins 1983: fig. 20), from which it is differs in being distinctly smaller, it also resembles the femur of *Nemegtbaatar gobiensis* (ZPAL MgM-I/81), as reconstructed by Kielan-Jaworowska et al. (2004: fig. 8.13), from which it differs in being larger, and *Kryptobaatar dashzevegi* ZPAL MgM-I/41 (Kielan-Jaworowska and Gambaryan 1994, several figures and personal observations). It differs from the femora of ?*Eucosmodon*, *Nemegtbaatar*, and *Kryptobaatar* in having the greater trochanter (as seen in lateral and medial views) anteriorly recumbent (Fig. 8A$_5$–A$_8$), rather than lying in prolongation of the shaft, and in having the neck of the femoral head more horizontally directed (Fig. 8A$_1$–A$_4$). In spite of the differences in size, the femora in these four taxa appear to be similarly stout in proportion to length and differ in this respect from the femora of e.g., *Mesodma* sp. (e.g., UMVP 1424 and MCZ 20776), figured by Krause and Jenkins (1983: fig. 21C, D), which appear relatively more slender. Both femora of *Catopsbaatar*, preserved in PM 120/107 differ from those belonging to all other taxa mentioned above in having the subtrochanteric tubercle hardly discernible. We regard this difference as due of the state of preservation of PM 120/107, in which all the longitudinal bones are strongly abraded and none of the processes has been preserved completely.

The estimated length of the *Catopsbaatar* femur, based on a comparison with that of ?*Eucosmodon* sp., *Nemegtbaatar gobiensis*, and *Kryptobaatar dashzevegi*, is about 56 mm.

?Parafibula.—The parafibula is a small ossicle in the knee joint, described in multituberculates (*Ptilodus*) by Krause and Jenkins (1983), and in *Kryptobaatar* and *Chulsanbaatar* by Kielan-Jaworowska and Gambaryan (1994). The latter authors argued (p. 64): "[...] m. gastrocnemius lateralis possibly originated in multituberculates from the parafibula (as in some marsupials), rather than from the femur as in eutherians."

In *Catopsbaatar catopsaloides* we found an uncertain parafibula in the left knee joint, as illustrated in Fig. 9A$_4$, A$_5$, and A$_7$.

Tibia.—The tibiae of Paleocene multituberculates were described by Gidley (1909), Granger and Simpson (1929), and Krause and Jenkins (1983), while those from the Cretaceous by Deischl (1964), and Kielan-Jaworowska and Gambaryan (1994). In PM 120/107 both fragmentary tibiae are preserved: the left one, nearly complete (no. 61 in Fig. 1A; see Fig. 9A), associated with the lateral femoral condyle and a tiny fragment of the femoral shaft; and a fragment of the right tibia (no. 38 in Fig. 1A, not figured separately herein) consisting of a partial, strongly flattened shaft. The description that follows is of the left tibia.

The tibia is about 35.8 mm long. The proximal extremity (Fig. 9A$_7$; Fig. 9B is the fibula), the medial part of which is badly damaged, originally had roughly oval outline, and its estimated mediolateral width (measured after removal of the medial femoral condyle) is about 11 mm; the anteroposterior length is about 7 mm. The hook-like lateral process has been broken, but the lateral elongation of the proximal extremity (Fig. 9A$_1$) shows its position. In anterior and posterior views (Fig. 9 A$_1$, A$_2$) the shaft extends longitudinally in the proximal part, the distal part being very gently bent medially. In medial and lateral views (Fig. 9A$_3$, A$_4$), the distalmost end of the shaft is bent laterally. The surface of the bone of the shaft is poorly preserved, in some places the compact layer is missing and the details of the shaft structure are difficult to discern.

As is characteristic of multituberculate tibiae (Kielan-Jaworowska and Gambaryan 1994), the mediolateral diameter of the tibia is considerably greater than the anteroposterior. This character may be best observed in the left tibia of ZPAL MgM-I/110, assigned by Kielan-Jaworowska and Gambaryan (1994) to *Nemegtbaatar gobiensis* and figured in their fig. 17F–I. In anterior and posterior views (Kielan-Jaworowska and Gambaryan 1994: fig. 17I and H respectively), the diameter of the medial part of the shaft of the tibia appears dramatically larger than in medial and lateral views (Kielan-Jaworowska and Gambaryan 1994: fig. 17F and G, respectively). Kielan-Jaworowska and Gambaryan (1994: 63) stated that in *Nemegtbaatar* (ZPAL MgM-I/110) the craniocaudal (anteroposterior) diameter of the tibia is 60% of the mediolateral diameter. In *Catopsbaatar* PM 120/170, as may be seen in Fig. 9A, the anteroposterior diameter in the middle of the shaft is 57% of the mediolateral (see also section *Discussion* at the end of this paper).

The tibial tuberosity, distinct in *Nemegtbaatar*, cannot be discerned. The anterior (cranial) border (sometimes termed crista tibiae) is weak but discernible in anterior view (Fig. 9A$_2$), and extends from the medial side of the anterior margin of the proximal extremity obliquely toward the middle of the shaft, as may be seen also on the tibiae of *Kryptobaatar* (ZPAL MgM-I/41, Kielan-Jaworowska and Gambaryan 1994: fig. 6C). It is not evident in nor described by Deischl (1964: pl. 8) in tibia of *Mesodma* sp., or in numerous tibiae of Paleocene multituberculates figured by Krause and Jenkins (1983: fig. 23A–D). In *Catopsbaatar* it is not discernible in the middle part of the shaft due to the damage, but discernible again more distally, extending longitudinally as a faint ridge in the distal part of the shaft, disappearing at the last fifth of the tibia length. The origin of the anterior crest from the medial side of the anterior border in multituberculates *Catopsbaatar* and *Kryptobaatar* (less evident in tibia of *Nemegtbaatar*) differs from those in eutherian mammals, where it extends from the lateral side of the anterior margin of the proximal extremity obliquely towards the middle of the shaft, rather than from the medial side of the proximal extremity (see various books of on anatomy of domestic animals and human anatomy, Getty 1975; Schaller 1992; Evans 1995; and many other text-books and papers).

In posterior view, the proximal part of the shaft just below the proximal extremity is deeply excavated, as characteristic of the tibiae described by Deischl (1964), and by Krause and

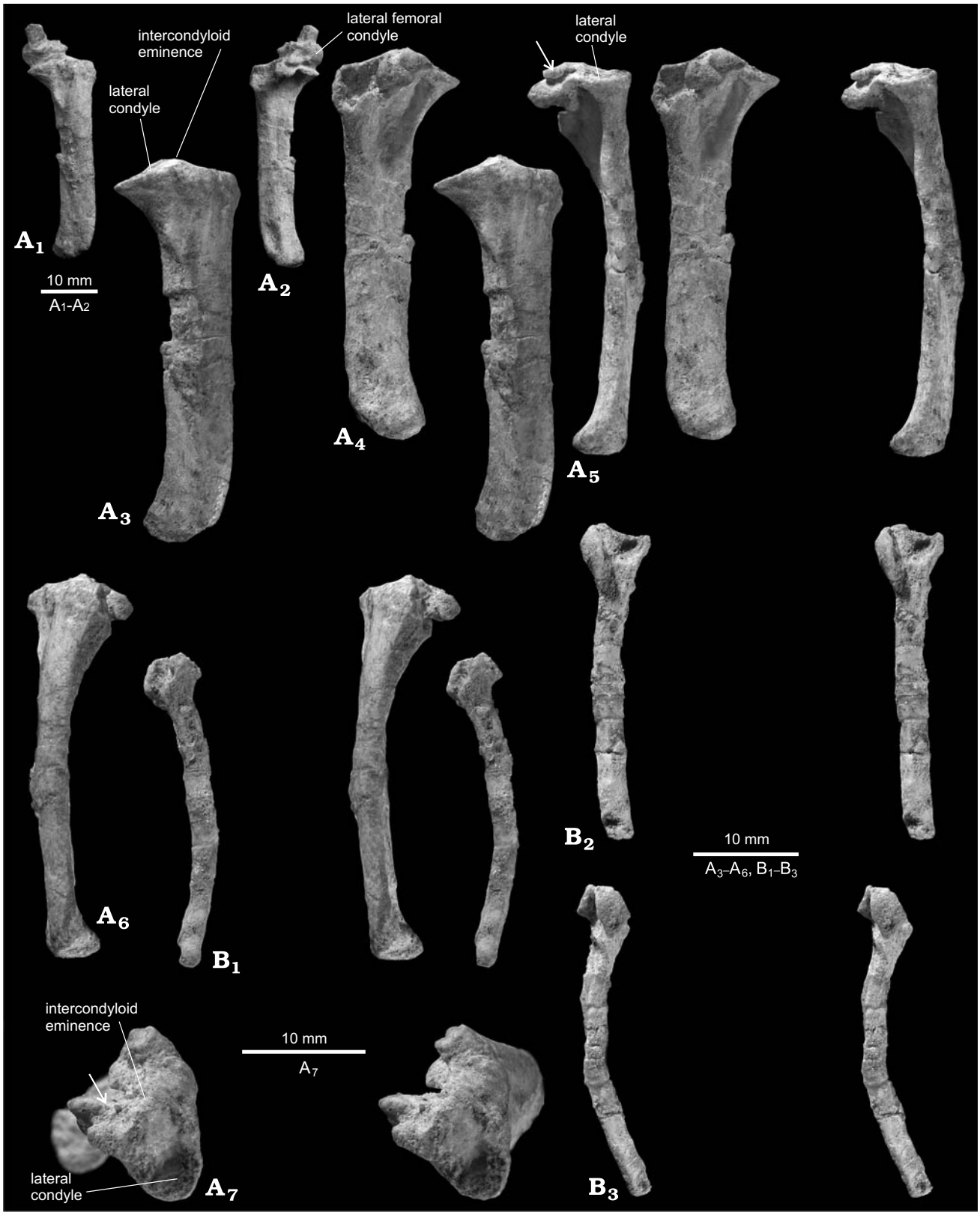


Fig. 9. Multituberculate mammal *Catopsbaatar catopsaloides* (Kielan-Jaworowska, 1974), PM 120/107, Upper Cretaceous, red beds of Hermiin Tsav, Hermiin Tsav I locality, Gobi Desert, Mongolia. **A**. Left tibia (no. 61 in Fig. 1B); A_1, A_2, left tibia with fragment of lateral femoral condyle and a tiny fragment of femoral shaft preserved on the proximal surface, in posterior (A_1) and anterior (A_2) views; A_3–A_5, higher magnification of the same tibia, after removal of femur's fragments, in posterior (A_3), anterior (A_4), lateral (A_5), and medial (A_6) views; A_7, still higher magnification of the same tibia in proximal view. The arrows in A_5 and A_7 denote the damaged ?parafibula. Note the damage of the medial part of the proximal surface. **B**. Left fibula (no. 62 in Fig. 1B) with strongly damaged proximal part in ?posterior (B_1), ?medial (B_2), and ?lateral (B_3) views. All except for A_1 and A_2 are stereo-photographs.

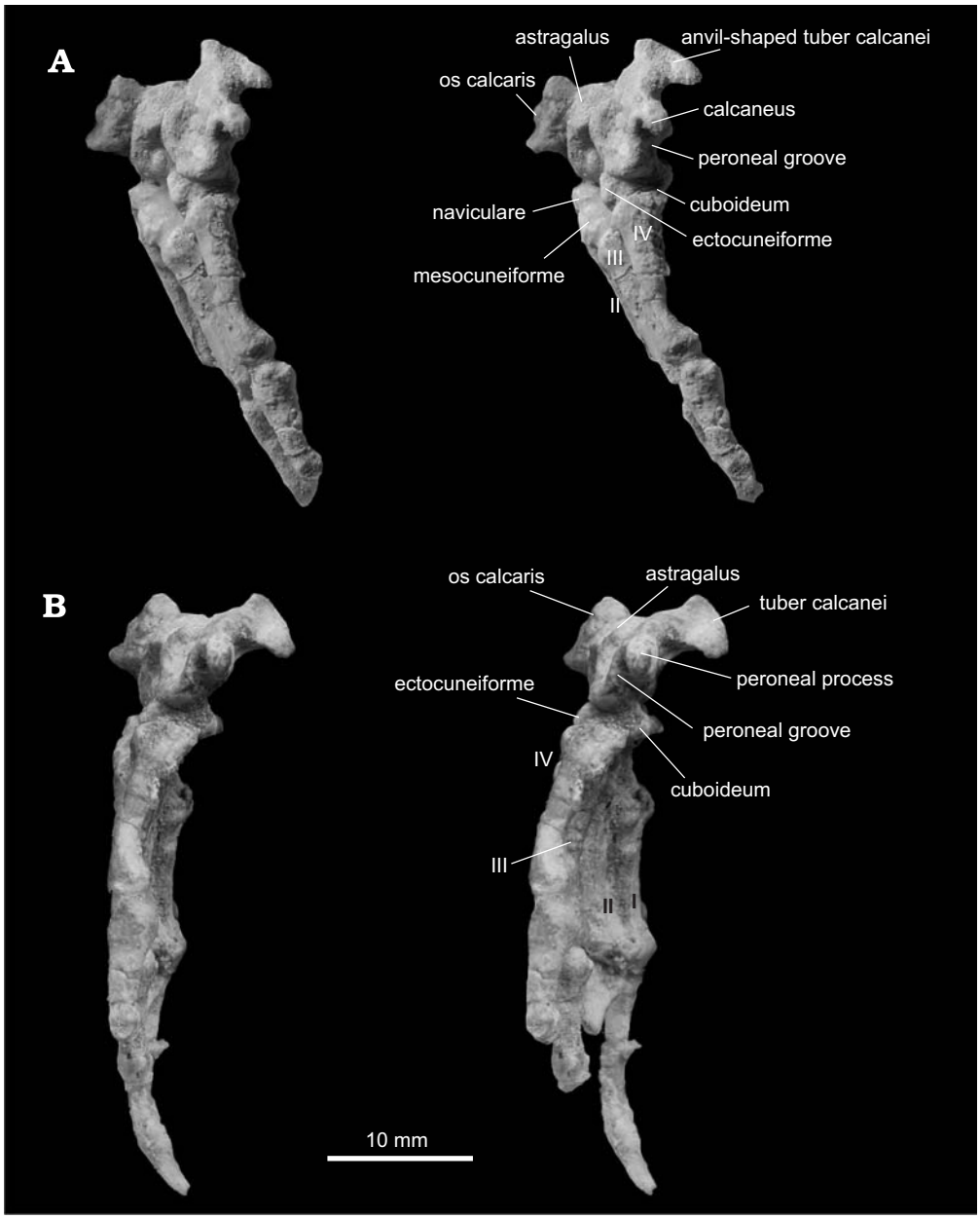


Fig. 10. Multituberculate mammal *Catopsbaatar catopsaloides* (Kielan-Jaworowska, 1974), PM 120/107, Upper Cretaceous, red beds of Hermiin Tsav, Hermiin Tsav I locality, Gobi Desert, Mongolia (nos. 66 and 69 in Fig. 1A and B respectively). Left tarsus of *Catopsbaatar catopsaloides* . **A**. Stereo-photograph in lateral view, with metatarsals arranged obliquely and calcaneus in lateral view. **B**. Stereo-photograph in lateral and in a slightly plantar view. The specimen in B looks larger than in A, because the first finger, preserved in B, has been removed from A.

Jenkins (1983). This excavation is probably characteristic of all multituberculate tibiae, but as this part has been poorly exposed in the specimens of *Kryptobaatar*, *Nemegtbaatar*, and *Chulsanbaatar*, studied by Kielan-Jaworowska and Gambaryan (1994), its relation to the insertion of a particular muscle (or muscles) has not been discussed by these authors. In the distal part of the posterior view of PM 120/107, there is a deep longitudinal groove, placed on the lateral side of the shaft (Fig. $9A_2$), probably caused by distortion.

In lateral view (Fig. $9A_5$) the shaft is rather smooth and gently bent posteriorly in the distal part. The medial view (Fig. $9A_6$) shows the same posterior bending of the distalmost part of the shaft; a sharp longitudinal ridge, dividing the anterior and posterior surfaces of the shaft, extends from the middle of the posterior margin of articular surface, all along the length of the shaft.

The distal articular surface is badly damaged, and the medial malleolus is not preserved.

Fibula.—The partial left fibula has been preserved in PM 120/107 (no. 62 in Fig. 1A and Fig. 1B), situated lateral to the tibia and parallel to it. The fibula is poorly preserved, the shaft being broken transversely into several small pieces that have been glued together, the fibular head is badly damaged and details of its structure cannot be discerned. In

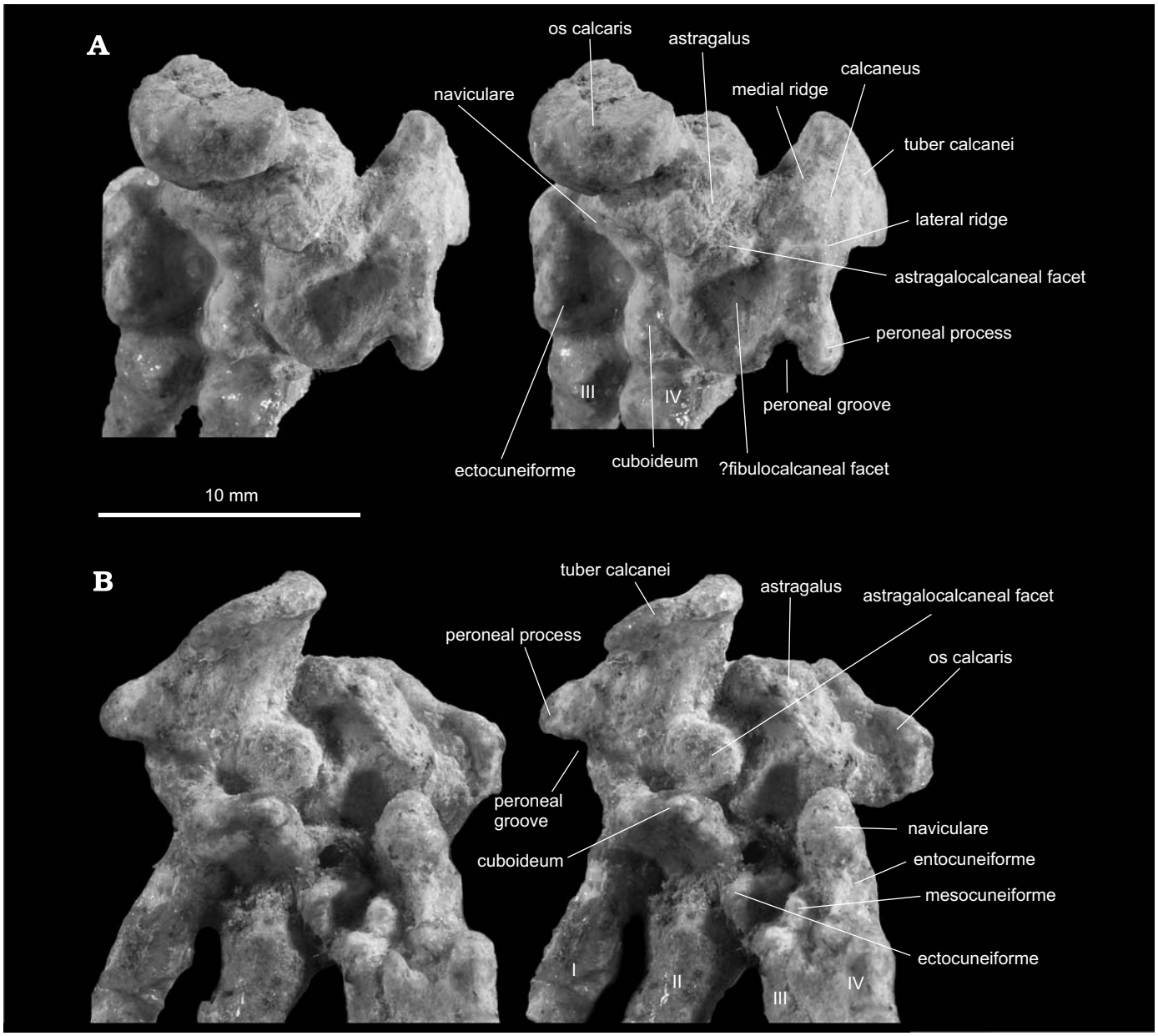


Fig. 11. Multituberculate mammal *Catopsbaatar catopsaloides* (Kielan-Jaworowska, 1974), PM 120/107, Upper Cretaceous, red beds of Hermiin Tsav, Hermiin Tsav I locality, Gobi Desert, Mongolia (nos. 66 and 69 in Fig. 1B). Detail of the left tarsus. **A**. Stereo-photograph in dorsal view. **B**. Stereo-photograph of the same in ventral view. Note that the metatarsals have been slightly distorted from their original place in the living animal.

spite of the poor state of preservation we figure the fibula in Fig. 9B, for the sake of completeness. The fibular shaft is bent and strongly convex laterally; the length of the preserved part along the chord is 30 mm.

Bones of the tarsus

Calcaneus.—The calcaneus of *Catopsbaatar* differs from the calcanei of other multituberculates and many other mammals in having a short tuber calcanei, bent laterally and ventrally, with an expanded proximal process. A more or less similarly-shaped tuber calcanei has been found in "*Tombaatar*" from the Upper Cretaceous of the Gobi Desert, studied by Minjin (2003). We do not re-figure the illustration of Hurum et al. (2006: fig. 4), but choose to show the left tarsus in detail in Figs. 10 and 11. We also figure here the isolated fifth left metatarsal associated with first phalange, the disarticulated right astragalus and the os cornu calcaris in Fig. 12.

The calcaneus preserved in PM 120/107 has been rotated medially from its original position, and is oriented nearly transversely (Figs. 10 and 11), so that in dorsal view of the tarsus, the distal end of the calcaneus (housing the peroneal groove) is arranged almost laterally rather than distally as characteristic of Multituberculata. The lateral side of the dorsal surface of the calcaneus in front of the peroneal process is bent latero-ventrally. The characteristic feature of the cal-

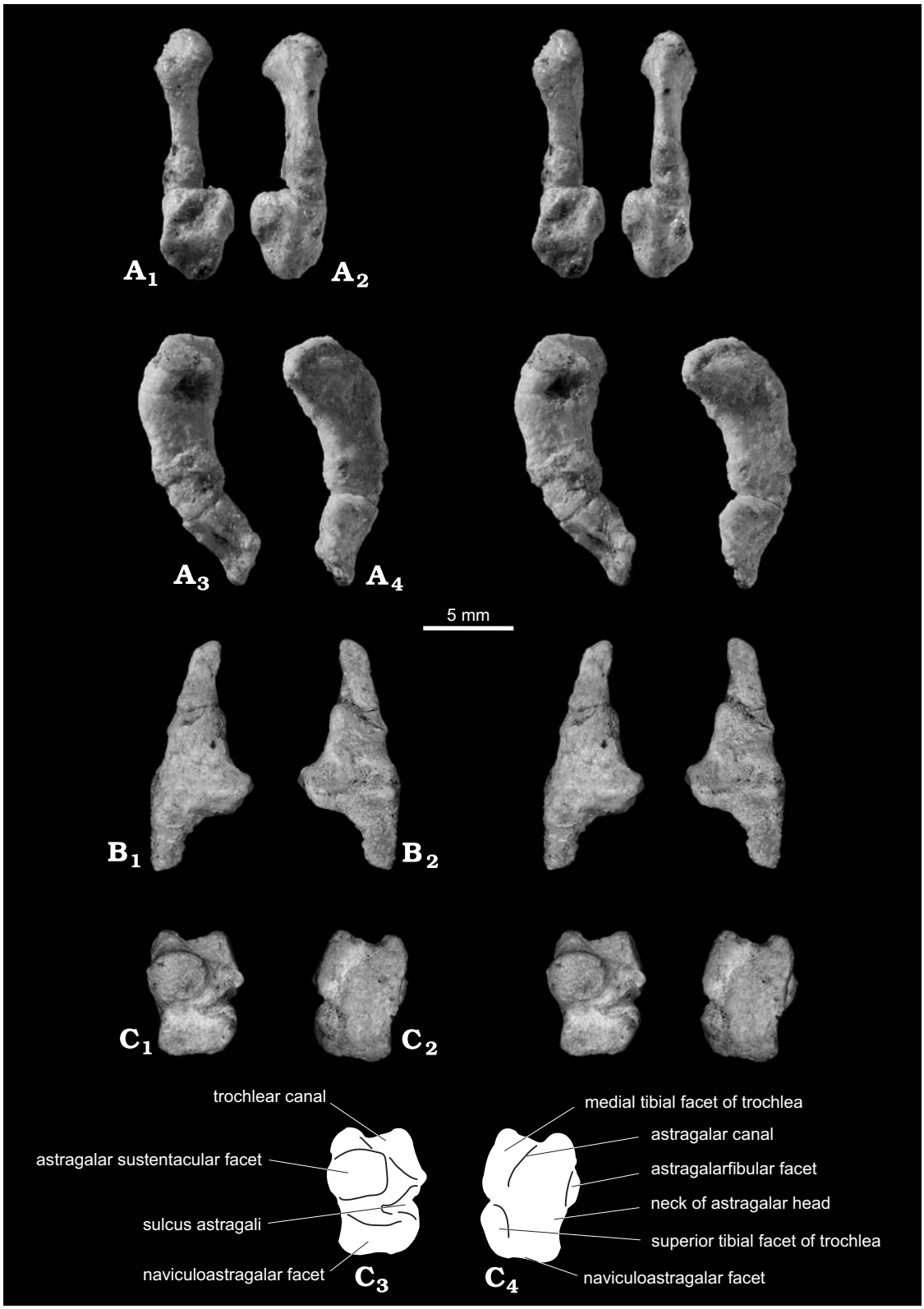


Fig. 12. Multituberculate mammal *Catopsbaatar catopsaloides* (Kielan-Jaworowska, 1974), PM 120/107, Upper Cretaceous, red beds of Hermiin Tsav, Hermiin Tsav I locality, Gobi Desert, Mongolia. Disarticulated bones of the tarsus. **A**. Left Vth metatarsal associated with the first phalange and not identified bone preserved on the plantar side of the phalange (no. 69 in Fig. 1B), in dorsal (A_1), plantar (A_2), medial (A_3), and lateral (A_4) views. Unidentified bone obscures the shape of the first phalange in all the views. Furrow for the tendon of m. peroneus longus, as a rule seen in proximal part of the plantar view of MtV in well preserved multituberculate skeletons, in figured specimen is hardly discernible because of the poor state of preservation. **B**. Os cornu calcaris (no. 30 in Fig. 1B), in dorsal (B_1) and ventral (B_2) views. **C**. Right astragalus (no. 71 in Fig. 1B), in plantar (C_1) and dorsal (C_2) views. A_1–C_2, stereo-photographs; C_3 and C_4, explanatory drawings for C_1 and C_2.

caneus is the shortness of the tuber calcanei, which is provided with an extensive anvil-shaped proximal process. At the horizontal position of the medial part of the calcaneus (e.g., in dorsal view of the entire tarsus, see Fig. 11A), the bent, lateral part of the tuber calcanei with anvil-shaped proximal process is not exposed. In such a view the tuber calcanei appears as a narrow process. In addition to the latero-ventral bending of the lateral part of the tuber calcanei, the whole anterior half of the dorsal surface of the calcaneus is also slightly bent antero-ventrally.

On the dorsal surface of the calcaneus there are two faint, thread-like ridges, one subparallel to the medial margin, extending from the astragalocalcaneal facet (see below) anteriorly and reaching the medial side of the anvil-shaped proximal process. The other faint ridge extends from the middle of the peroneal groove anteromedially, in a bow slightly convex anteriorly, and reaches the first ridge (Fig. 11). The astragalocalcaneal facet, obscured by the astragalus, which fits tightly to calcaneus, is seen in the dorsal view of the calcaneus (Fig. 11A) as a slight swelling convex medially, at the medial margin of the calcaneus. Lateral to the astragalocalcaneal facet on the dorsal surface of the calcaneus there is a large, rounded concavity (designated herein a fibulocalcaneal facet).

In lateral view of the calcaneus (Fig. 10A), the bent part of the tuber calcanei is arranged obliquely rather than anteriorly (longitudinally) with respect to the basis of the calcaneus; in relation to this, the anvil-shaped proximal process is arranged obliquely, anteromedially / posterolaterally to the medial margin of the calcaneus, rather than at a right angle with respect to it. The bent lateral part of the tuber calcanei in lateral view is roughly triangular and protrudes laterally over the lateral margin of the calcaneus; the margin between the anvil-shaped process and the peroneal process is concave, with a small convexity at the middle of its length.

In ventral view of the tarsus (Fig. 11B) the anvil-shaped proximal process of the tuber calcanei strongly protrudes ventrally and is arranged obliquely anteromedially / posterolaterally. The calcaneus in this view has irregular structure, with a large rounded surface of the astragalocalcaneal facet seen in medioventral part of the calcaneus. The extensive peroneal process is situated at the anterolateral corner of the calcaneus; medial to it on the distal margin, the peroneal groove is discernible, poorly seen in this view.

Because of the poor state of preservation of the surface of the calcaneus in PM 120/107, we refrain from recognition of other facets.

Astragalus.—In dorsal view of the tarsus (Fig. 11A) the astragalus is irregular, being placed obliquely lateroproximally / mediodistally, covering the calcaneus with its proximal end, contacting the naviculare mediodistally and the cuboideum laterally. Its medial margin is partly obscured by the os calcaris, which covers it dorsally. The disarticulated right astragalus (Fig. 12C) shows a large trochlea for the tibia, with a well developed trochlear groove, a large round astragalar sustentacular facet, a constricted neck and a well developed naviculoastragalar facet. The sulcus astragali is shallow and the dorsal side of the bone is almost smooth with a large medial tibial facet.

The extratarsal spur.—The os calcaris in *Catopsbaatar* and its use as a support for the cornu calcaris were described by Hurum et al. (2006: fig. 4). After further preparation of the specimen the ossified cornu calcaris has been found. The bone is given the number 63 in Fig. 1B. It is triangular in shape, and its posterior margin is obliquely placed and has a concavity in the middle, seen in both dorsal and ventral views (Fig. 12B). The maximum length of the bone is 13 mm, the maximum width 5 mm. The spur is flattened and at the cornu-os junction the bone is thicker and possesses several ridges for the attachment to os calcaris. The side with the attachment surface we designate the ventral side. The os calcaris bears corresponding ridges and grooves on its dorsal surface (Fig. 11A). As the os calcaris has possibly moved from the plantar to the medial side of the metatarsus it is not possible to tell if the spur was originally oriented medially, as it is in extant monotremes. The ossified cornu calcaris bears no impression for a venom canal.

Discussion

The extratarsal spur

Compared to the fused os calcaris and the ossified cornu calcaris in other Mesozoic mammals like *Gobiconodon* and *Zhangheotherium* (see Hurum et al. 2006), the multituberculates so far described differ in the lack of fusion between the two elements. All Mesozoic mammals most probably possessed keratinous spurs covering the ossified cornu calcaris. But there are no impressions on the ossified cornu calcaris in any specimen that corresponds to a canal for venom. The extant monotremes do not have the ossified cornu calcaris but retain the os calcaris and the hollow, keratinous cornu calcaris.

The pelvis

The lack of fusion of the left and right ischia is very different from the fused keel in *Kryptobaatar dashzevegi* (ZPAL MgM-I/41) described by Kielan-Jaworowska (1997) and Kielan-Jaworowska and Gambaryan (1994: fig. 2). The unfused sutures for ilium/ischium, pubis/ischium and pubis/ilium are also different from what is observed in *Kryptobaatar dashzevegi* (ZPAL MgM-I/41) and *Nemegtbaatar gobiensis* (see Kielan-Jaworowska and Gambaryan 1994: figs. 2 and 16F). There are three different plausible explanations for this. Either the fusion of the pelvis was a late stage in the development of *Catopsbaatar*, or it is a result of sexual dimorphism and occurs only in females, or it represents a taxonomically significant difference between *Catopsbaatar* and the two other taxa in which the pelvis is known.

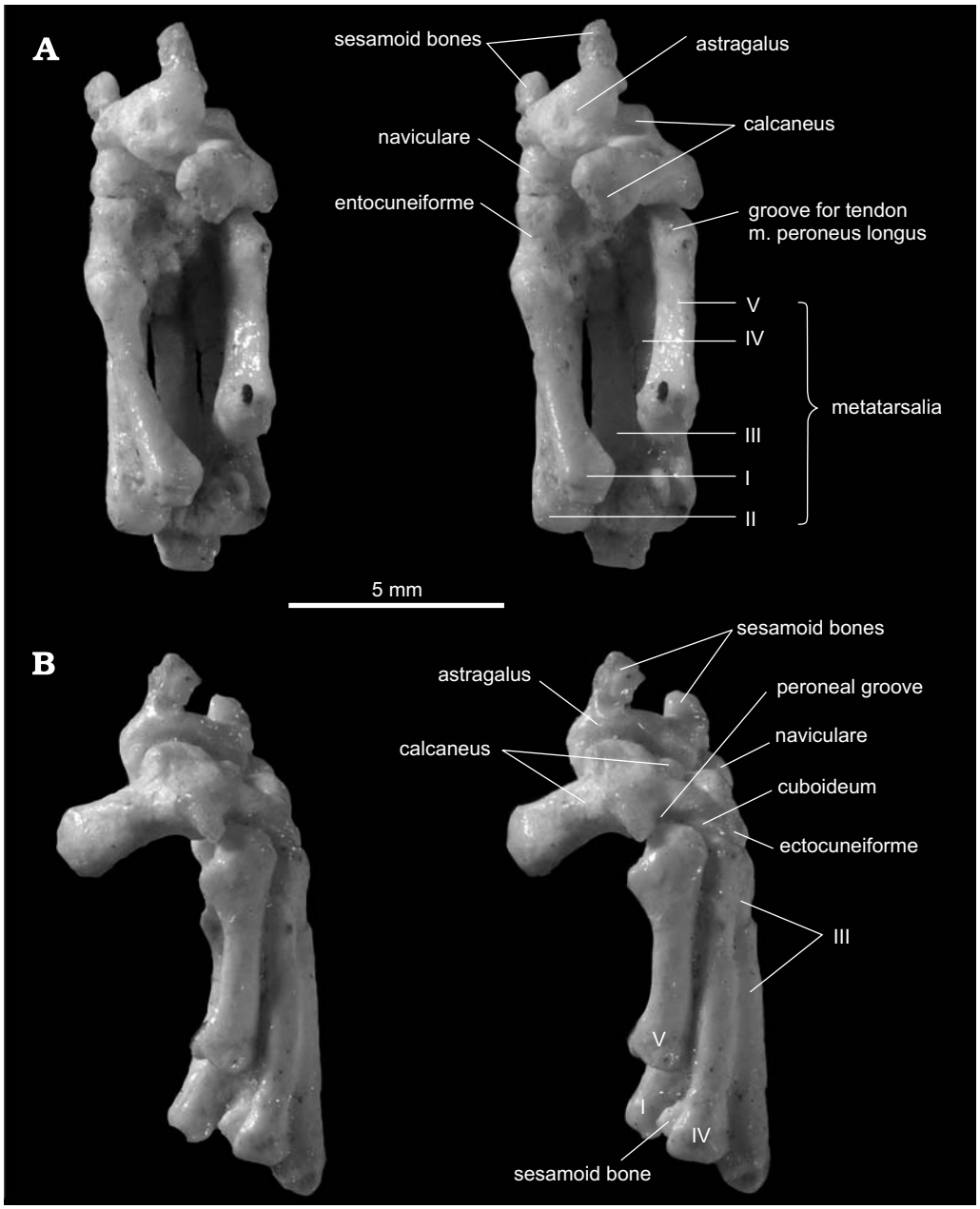


Fig. 13. Right tarsus of multituberculates mammal *Kryptobaatar dashzevegi* Kielan-Jaworowska, 1970, ZPAL MgM-1/41. Upper Cretaceous, ?Early Campanian Djadokhta Formation, Bayan Zak, Gobi Desert, Mongolia. Stereo-photographs in plantar (**A**) and lateral (**B**) views.

The presence of sutures suggests that PM 120/107 is a juvenile specimen, but the skull of this specimen described by Kielan-Jaworowska et al. (2005) does not confirm its young age. This lack of a rounded smooth surface anteriorly in the ischia forming a part of the acetabulum is also difficult to explain, but if it is a juvenile it might indicate an acetabulum formed of a cartilage. The authors know of no mammal where the ischia are excluded from the acetabulum and will not claim such an extreme statement from just one specimen. Considering the small number of pelvic girdles known in multituberculates, sexual dimorphism cannot be ruled out as an explanation. Conceivably, the males had a fused pelvic girdle, while the females retained an earlier ontogenetic stage (unfused condition) to accommodate the need for an expandable birth canal. It cannot be also excluded that the observed differences are of specific character, as however, there are so few specimens, such conclusion must remain unresolved.

Structure of the multituberculate tarsus

The structure of the multituberculate tarsus has been a matter of controversy. Granger and Simpson (1929: fig. 23) offered the first reconstruction, based on nearly complete, but isolated tarsal elements of *Eucosmodon* sp. (AMNH 16325) from the early Paleocene of New Mexico. This reconstruction was based, among others, on presence of distinct calcaneo-cuboid

facets, preserved on the calcaneus and the cuboid. The facets demonstrated that the cuboid did not articulate with the distal end of the calcaneus (as is characteristic of Theria), but rather with a facet placed obliquely (almost longitudinally) on the distal portion of the medial wall of the calcaneus. If this reconstruction were correct, the multituberculate tarsus would be prone to dislocation, as the calcaneus, not supported distally by a bone or cartilage, might lose the calcaneocuboid contact and slide laterodistally out of its normal position during the eversion of the foot.

The gap between the distal end of the calcaneus and the fifth metatarsal, as reconstructed by Granger and Simpson (1929) for multituberculates, occurs also in bauriamorphs and cynodonts (Schaeffer 1941a, b; Jenkins 1973; Szalay 1993). Schaeffer (1941a), however, argued on the basis of an X-ray of the pes of *Bauria*, that the gap between the distal end of the calcaneus and the fifth metatarsal might be filled either by a lateral fibrocartilaginous extension from the cuboid, or by a persistent, cartilaginous fifth tarsal (see also Kielan-Jaworowska 1997: fig. 5, and discussion therein).

Krause and Jenkins (1983) described all postcranial materials of North American multituberculates then known. Among the material studied by them, the most complete and best preserved is a nearly complete skeleton of *Ptilodus kummae* Krause, 1977 (UA 9001) from the upper Paleocene Ravenscrag Formation, Saskatchewan, Canada. None of the described specimens preserved the tarsus in anatomical arrangement. In *P. kummae* (Krause and Jenkins 1983: figs. 7 and 27), the well preserved right tarsus consists of displaced calcaneus and astragalus, the remainder of the tarsal bones plus all the metatarsals being placed at some distance more distally, at an angle of about 90° with respect to the displaced calcaneus. Metatarsal V is well preserved and shows a proximal margin that is convex posteriorly (rather than flat as in other metatarsals). In ventral view (Krause and Jenkins 1983: fig. 27B), the distinct groove for the tendon of m. peroneus longus (see below) is discernible in the proximal part of metatarsal V. Krause and Jenkins also (1983: fig. 24) provided photographs of all the tarsal elements and the pes of *Eucosmodon* sp. (AMNH 16325), placed in anatomical arrangement, which retains the pattern reconstructed earlier by Granger and Simpson (1929) for this specimen.

Based on study of multituberculate tarsi from the Campanian of the Mongolian part of the Gobi Desert, Kielan-Jaworowska and Gambaryan (1994), and Kielan-Jaworowska (1997) challenged the reconstruction of Granger and Simpson (1929), arguing that the posteriorly convex proximal margin of the fifth metatarsal articulated with the peroneal groove on the distal end of the calcaneus. Four multituberculate tarsi are known from the Campanian (Djadokhta or Baruungoyot formations) of the Mongolian part of the Gobi Desert, three of which are housed in the ZPAL collection and one in the PM collection. These are:

(1) ZPAL MgM-I/41, the right tarsus of *Kryptobaatar dashzevegi* Kielan-Jaworowska, 1971, from the Djadokhta Formation, Bayan Zak, Gobi Desert, preserved in anatomical arrangement with nearly complete hind limbs, pelvis, parts of the vertebral column, plus skull and partial dentaries. This specimen was described and figured by Kielan-Jaworowska and Gambaryan (1994: figs. 2A, 5A, 6A–C, 7), and is re-figured herein (Fig. 13). In that figure we provide the enlarged photo of that tarsus in lateral view, similar to the position figured by Kielan-Jaworowska and Gambaryan (1994: figs. 6B and 7D) and in ventral view (not figured previously, showing the horizontal groove for the tendon of m. peroneus longus, on the plantar side of MtV, close to the proximal margin. In this specimen the joint between the distal end of the calcaneus and the proximal end of metatarsal V is well preserved, the convex (almost pointed) proximal margin of the fifth metatarsal entering the peroneal groove of the calcaneus.

(2) ZPAL MgM-I/41, the left tarsus of the same specimen, in which, however, the distal part of the calcaneus is missing, and the calcaneo-metatarsal joint not preserved (Kielan-Jaworowska and Gambaryan 1994: figs. 2B, 5A, 6C, D).

(3) ZPAL MgM-I/99b, the left tarsus of *Chulsanbaatar vulgaris* Kielan-Jaworowska, 1974, from red beds of Hermiin Tsav, Hermiin Tsav II, Gobi Desert, Mongolia, described and figured by Kielan-Jaworowska and Gambaryan (1994: fig. 25) showing the calcaneometatarsal V contact.

(4) PM 120/107, the left tarsus of *Catopsbaatar catopsaloides* (Kielan-Jaworowska, 1974), from red beds of Hermiin Tsav, Hermiin Tsav I, Gobi Desert, Mongolia, with metatarsal V, preserved separately, figured by Kielan-Jaworowska et al. (2002: fig. 1); Hurum et al. (2006: fig. 4) and figured in more detail herein (Figs. 1 and 8–11). The isolated metatarsal V, associated with a phalanx, is similar to those in other Late Cretaceous Mongolian specimens.

In addition to the above mentioned Late Cretaceous tarsi, which are the best preserved, the right multituberculate tarsus IVPP V12517, belonging to *Sinobaatar lingyuanensis* Hu and Wang, 2002a is known from the Lower Cretaceous Yixian Formation (Jehol Biota) of Liaoning Province, China. The specimen has been so far figured only in ventral view (Hu and Wang 2002a: fig. 2B; and 2002b, the same figure numbered 2d) and briefly described. Hu and Wang (2002b: 936) stated: "The proximal end of metatarsal V articulates with the distal end of the cuboid, without contact with the calcaneus". Hu and Wang commented (2002b: 936) that metatarsal III is parallel to the calcaneus in the foot of *Sinobaatar*. This foot structure, in their opinion, resembles feet of *Ptilodus* and *Eucosmodon* sp., as reconstructed by Granger and Simpson (1929) and Krause and Jenkins (1983), and is different from the reconstruction offered by Kielan-Jaworowska and Gambaryan (1994).

Hu and Wang (2002b: 936) further stated: "Kielan-Jaworowska and Gambaryan argued that, in multituberculates, the metatarsal V articulated with the distal end of calcaneus, and the longitudinal axis of metatarsal III intersected that of the calcaneus at about 30° outwards. However, the metatarsal V on the specimen (ZPAL MgM-I/96b), based on the fact which the foot morphology is reconstructed, does not exceed

the distal end of the cuboid [...]". The authors apparently meant the specimen of *Chulsanbaatar vulgaris* ZPAL MgM-I/99b (rather than 96b as cited), figured by Kielan-Jaworowska and Gambaryan (1994: fig. 25). This figure, however, is not a reconstruction, but a camera lucida drawing of the specimen ZPAL MgM-I/99b.

The structure of the tarsus in *Sinobaatar* (as far as can be judged from the published evidence) appears to be rather different from that in Late Cretaceous multituberculate tarsi, which might be due to the considerable displacement of the bones in the specimen of *Sinobaatar*. We thoroughly examined an enlarged photograph from Hu and Wang (2002a: fig. 1B), which shows the apparent, shallow peroneal groove on the distal end of the calcaneus, into which fits the proximal end of the cuboid (which is unusual, as in all other multituberculates the cuboid articulates with the distal part of the medial wall of the calcaneus). The distal, extensive end of the cuboid articulates not only with the proximal end of metatarsal V, but apparently also with a part of the proximal end of metatarsal IV. Not having an opportunity to examine the original specimen IVPP V12517 of *Sinobaatar*, we refrain from further commenting on it, pending publication of its more detailed description and illustrations.

The characteristic feature of the four Late Cretaceous Mongolian tarsi (listed above) is the structure of metatarsal V, the proximal margin of which is convex posteriorly, sometimes even pointed, rather than being transverse (as in the remaining metatarsals). Kielan-Jaworowska and Gambaryan (1994) demonstrated that the anterior convex end on MtV articulated with the peroneal groove on the calcaneus. This is clearly shown in the two best preserved specimens: the right tarsus of *Kryptobaatar dashzevegi* (Fig. 13) and the left tarsus of *Chulsanbaatar vulgaris* (Kielan-Jaworowska and Gambaryan 1994: fig. 25). In both these specimens the calcaneometatarsal V contact is preserved in nearly original position, although in both the tuber calcanei has been slightly displaced laterally. In all the multituberculate metatarsals V available to us, on the plantar side of the metatarsal V there is a distinct subtransverse groove for the tendon of m. peroneus longus, as figured by Kielan-Jaworowska and Gambaryan for *Kryptobaatar* and *Eucosmodon* (1994: figs. 54B and 57B respectively). Such a groove is also present in *Ptilodus kummae* (UA 9001) figured by Krause and Jenkins (1983: fig. 27).

The characteristic feature of all known multituberculate calcanei is a deep groove for the tendon of m. peroneus longus, on the lateral side of the distal margin of the calcaneus, which separates the peroneal process from the calcaneal body. The size, width, and shape of the groove for the tendon of m. peroneus longus and of the peroneal process vary among the known multituberculate calcanei. Szalay (1993), and Kielan-Jaworowska and Gambaryan (1994) hold that the groove transmitted the tendon of m. peroneus longus from the dorsal to the plantar side of the calcaneus. In this respect the multituberculate tarsus differs from those in eutherian mammals (see e.g., various text books of human and/or veterinary anatomy), in which there is no groove for the tendon of m. peroneus longus on the calcaneus. As generally known, in eutherians the cuboid distally articulates with the calcaneus, and the tendon of m. peroneus longus passes to the plantar side of the tarsus, usually by encircling the cuboid laterally. It then extends medially on the plantar side, along the distal margin of the cuboid, ectocuneiform, and mesocuneiform, leaving grooves on all these bones, and inserts on the posterolateral plantar aspect of the mesocuneiform and the lateral side of metatarsal I, or on the medial aspect of metatarsal II and the lateral aspect of metatarsal I. There is considerable variability in its course in different representatives of eutherian mammals and details may vary.

In marsupials, in contrast to eutherians, there occurs a groove for m. peroneus longus on the calcaneus, differently developed in various taxa, sometimes missing (Szalay 1994). It is generally well developed in Cretaceous Ameridelphia (known from isolated bones, see numerous photographs and drawings in Szalay 1994) and more reduced or sometimes tending to disappear in Australidelphia. In Marsupialia (as in all Theria) the calcaneus is supported distally by the cuboid, and even if the tendon of m. peroneus longus passes on the plantar side of the tarsus by the peroneal groove, the further course of the tendon is certainly different than in multituberculates, where the calcaneus contacts distally the fifth metatarsal.

In addition to the groove on the plantar side of metatarsus V, the grooves for the tendon of m. peroneus longus have been best preserved in *Eucosmodon* sp. (AMNH, 16325), on the cuboid (see Kielan-Jaworowska and Gambaryan 1994: fig. 56 G) and other tarsal and metatarsal bones, as reconstructed by these authors in their fig. 57B.

If the reconstruction of the multituberculate tarsus by Granger and Simpson (1929) were correct, it would be difficult: (1) to explain the preservation of *Kryptobaatar* (Fig. 13) and *Chulsanbaatar* tarsi, in which the pointed end of the metatarsal V fits the groove for the tendon of m. peroneus longus in the calcaneus, (2) to explain the reason for the development of the convex, or pointed anterior margin in metatarsal V, and (3) to visualize the course of the tendon of m. peroneus longus after it leaves the peroneal groove on the plantar side of the calcaneus, as it would have had to extend along the soft parts, not being supported by a bone, which would be unusual for mammals.

The peculiar short and wide tuber calcanei described in *Catopsbaatar* (herein) and in a new genus related to *Tombaatar* (Minjin 2003) occurs also in several species of tree kangaroos *Dendrolagus*, however, in none of them, there is such an extensive and anvil-shaped proximal process of the tuber calcanei. The short and wide tuber calcanei and hence a short load arm is interpreted in adapiformes (primitive Primates) as an indication of quadrupedal and not leaping locomotion (Gebo 2002). The correct interpretation for this structure in *Catopsbaatar* and *Tombaatar* is difficult to assess. Maybe these two multituberculates were not jumping like e.g., *Nemegtbaatar* and *Kryptobaatar* (Kielan-Jaworowska

and Gambaryan 1994), but contrary to this evidence the long spinous process in a single lumbar vertebra in *Catopsbaatar* is indicative of jumping. Due to the fragmentary preservation of the described *Catopsbaatar* postcranial skeleton this question will remain unresolved until the complete postcranial skeleton of *Tombaatar* is described.

As a result of the above considerations and the evidence presented in this paper, we support the reconstruction of the multituberculate tarsus presented by Kielan-Jaworowska and Gambaryan (1994).

Conclusions

The partial postcranial skeleton of *Catopsbaatar* PM 120/107 shows generally the same pattern as other Late Cretaceous multituberculates from the Gobi Desert like *Chulsanbaatar, Kryptobaatar*, and *Nemegtbaatar*. We concur with conclusion of Kielan-Jaworowska and Gambaryan (1994) that at least dajdochtatherioid multituberculates had long spinous and transverse processes of the lumbar vertebrae (contra Sereno 2006) and with their reconstruction of the multituberculate tarsus (contra Hu and Wang 2002b). The calcaneus of *Catopsbaatar* is unusual, differing from calcanei of the majority of multituberculates known thus far (and many other mammals). The biological significance of the unusual tuber calcanei is unclear: as a working hypothesis, we suggest that it may speak for the presence of strong flexors that attach to the tuber calcanei, and perhaps to some saltatory ability in *Catopsbaatar*.

In *Catopsbaatar* the tarsus with os cornu calcaris and os calcaris has been found for the first time in multituberculates. The bones show no fusion and this is possibly a derived state compared to the two fused bones in other Mesozoic mammals (for a description of the os calcaris and os cornu calcaris in other early mammal taxa see Hurum et al. 2006).

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